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Cladistics of the *Aleiodes* Lineage of the Subfamily Rogadinae (Hymenoptera: Braconidae)

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Abstract.—A cladistic analysis was made for 208 *Aleiodes* species. Seventy three characters were examined. Host association data from literature and museum specimens were mapped onto the cladogram. The genus consists of 18 species-groups within three sections: basal, intermediate, and derived. Basal and intermediate species tend to be generalist feeders while derived species tend to attack noctuids. The monophyly of seven subgenera was discussed, which were subsumed under *Aleiodes*.

The purpose of this research was to provide a cladistic analysis of world species of *Aleiodes* Wesmael 1838, which could be used to interpret patterns of host-use by these wasps. Particular attention was given to defining species-groups by way of cladistic analysis based on morphological characters. Host association data was mapped onto the cladogram to determine any associations between parasitoid phylogeny and host-utilization. Such associations might indicate coevolutionary patterns within host-parasitoid relationships that developed over evolutionary time.

Efforts have also elucidated intergeneric relationships within subfamily Rogadinae, as well as interspecific relationships within *Aleiodes* (Achterberg 1991, 1993b; Shaw 1983, Shaw 1993, Shaw 1994, Shaw *et al.* 1997, Whitfield 1992). For many years there has been confusion about the definitions of the genera *Aleiodes* and *Rogas* Nees von Esenbeck. This problem has been clarified by Achterberg (1982, 1991), Achterberg and Penteado-Dias (1995), Shaw (1993) and Shenefelt (1969).

Morphological synapomorphies which define the subfamily: Rogadinae are: 1) propodeum either without distinct area superomedia, or if present, small; 2) dorsal carinae of metasomal tergite I converging posteriad; 3) metasomal tergites II and III well sclerotized and with extensive, distinct surface sculpturing (Shaw 1995).

The following features define *Aleiodes* as monophyletic: 1) basal portion of tarsal claw rounded with a pectin of spines (Shaw 1995); 2) tergite II carinate and anteromedial area with a polished triangular region that continues posteriad as a median carina (Shaw 1995); 3) median carina of propodeum never forking in anterior half of the segment and never diverging posteromedially into an areola (Shaw 1995); 4) fore wing RS+MB vein long (Shaw 1995); 5) emergence hole from host mummy even and circular (Shaw 1995); 6) ovipositor sheath widened and flattened (Achterberg 1991).

Most Rogadini appear to be solitary parasitoids, but two gregarious species are known (*A. stigmator* (Say), *A. pallescens* Hellen). As far as known, most *Rogas* species attack Limacodidae, Lycaenidae, Riodinidae, and Zygaenidae (Shaw, 1995). *Aleiodes* species utilize a wide variety of hosts (Shenefelt 1975; Shaw and Huddleston 1991, Shaw 1995).

Aleiodes usually glue their host mummies to a substrate by way of a hole chewed in the ventral area of the host prothorax. Emerging *Aleiodes* adults cut an emergence hole at the posterior end of the mummified caterpillar (Shaw 1995).

Aleiodes is a useful group of parasitoids for comparative studies for three reasons: 1) the physiological character of host mummification preserves the host for taxonomic study; 2) the genus is relatively species-rich, and thus offers a large sample of species with which to carry out a phylogenetic analysis; 3) in general, *Aleiodes* species tend to have narrow host ranges (Shaw 1994), yet across the genus, a wide variety of lepidopteran groups are attacked.

METHODS AND MATERIALS

Characters and character states.—Two hundred eight *Aleiodes* species were analyzed. A list of 62 evolutionary transformation series (Hennig 1966, Mickevich 1982, Mickevich and Weller 1990, and Wiley 1981) including 73 characters (numbered 0–72) and component character states, was derived from *Aleiodes* specimens examined (see Character Summary). Terms used to describe sclerite sculpturing features follow those of Harris (1979), while those used for sclerites and appendages follow Huber and Sharkey (1993). Wing venation terminology follows Shaw *et al.* (1997).

The characters used fell under two general categories: qualitative and morphometric. Qualitative categories included 1) sculpturing on specific sclerites, 2) shape of specific sclerites, 3) presence or absence of setation on specific body parts, 4) presence or absence of tarsal claw features, 5) presence or absence of specific wing veins, and 6) coloration. Morphometric categories included 1) number of flagellomeres, and 2) morphometric ratios of sizes of parts, or distances between parts.

Species included in the study.—Descriptions of each character are included below (Character Summary). Appendix I lists the *Aleiodes* species analyzed, including host information. The following species of *Rogas,* the putative sister-group of *Aleiodes* (Whitfield 1992) were used for outgroup comparison to best estimate polarization of transformation series for each character: *R. discoideus* (Cresson), *R. fusciceps* (Cresson), and *R. bucculatricis* (Ashmead). Four unnamed morphospecies of *Clinocentrus* Haliday were also used, as well as the following *Stiropius* (Whitfield) species: *S. bucculatricis* (Ashmead) and *S. californicus* Whitfield.

Character polarization.—*Aleiodes* character states which most closely resembled those of *Rogas, Stiropius,* and/or *Clinocentrus* (Whitfield, 1992) were hypothesized to resemble most closely the ancestral state (Hennig, 1981). For those characters for which there was significant, consistent departure in the *Rogas* state in comparison to the *Aleiodes* state(s), the latter two genera were examined to determine whether the *Aleiodes* or *Rogas* condition should be considered ancestral. If a given character state for *Rogas* species departed from that of *Stiropius* species, *Clinocentrus* species, and *Aleiodes* species, it was hypothesized to be derived. The state the latter three genera expressed in common was then hypothesized to be the ancestral state. If a given state expressed by *Stiropius* species departed from one that *Aleiodes* and *Clinocentrus* held in common, but not *Rogas,* and the *Rogas* state differed from the *Stiropius* state, the state that *Aleiodes* and *Clinocentrus* shared was hypothesized to be ancestral to *Aleiodes,* and the other two were hypothesized to be independently derived autapomorphies with respect to the four genera taken together. For cases in which a *Rogas* state was hypothesized to be derived, *Stiropius* was hypothesized to be more closely related to the ancestor of *Rogas* + *Aleiodes* than *Clinocentrus* (Whitfield 1992).

Ordering transformation series.—The ordering of character states with respect to one another was determined by polarization based on the hypothetical ancestor, as described above, and parsimony, as follows: For those transformation series with more than one state, once the ancestral state was hypothesized, various combinations of states for a given transformation series were tested with the Hennig86 phylogenetic analysis program (Farris 1988) as described in the next section. The ordering of character states for the character in question on the most parsimonious Nelson consensus tree among those derived from respective Hennig86 runs was hypothesized to represent the best estimation of phylogeny for that transformation series. All characters in this study consist of ordered character states. The Nelson consensus provides a strict consensus tree from equally parsimonious trees derived from a Hennig86 run. Exceptions to assigning '0' to the ancestral state were the following classes of hypotheses: 1) bipolar linear evolutionary transformation series, in which character states evolved in two directions from the ancestor, diagrammed thus:

$$a \leftarrow b \rightarrow c$$

and reticulate transformation series (Mickevich 1982, Mickevich and Weller 1990), in which either *i)* character states were hypothesized to have evolved from more than two directions from the ancestor, and/or *ii)* the ancestral character state for a given *Aleiodes* lineage or closely related lineages was an *Aleiodes* character state other than the ancestral *Aleiodes* character state for that entire transformation series.

We adopted the method of TSA for treating complex multi-state characters such as vertex sculpturing (Shaw *et al.* 1997), tarsal claw form, clypeal carina shape, propodeum sculpturing (Shaw *et al.* 1997), mesopleuron sculpturing, metasomal tergite sculpturing, and hind wing RS vein shape (Achterberg 1993a). This method has been described by Lipscomb 1992, Mickevich and Lipscomb 1991, and Mickevich and Weller 1990, and is commonly used (Lipscomb 1992, Mitter and Silverfine 1988, and Schuh 1991). It has been critiqued by Lipscomb (1992).

Alternate arrangements of character states of transformation series, in which more than one arrangement was possible, and it was not obvious from morphology alone how these character states were most logically ordered, were tested using Hennig86 program 1.5 (Farris, 1988) on a Dell Omniplex 466 system, to find the most parsimonious scheme for each respective reticulate transformation series. The most parsimonious scheme was then incorporated into the matrix.

The matrix and execution of the phylogenetic analysis.—An integer matrix (Table 1) based on integers representing coding for the states of the characters (see Character Summary), arrayed with the hypothetical ancestor and *Aleiodes* species in rows and characters in columns was analyzed by computerized algorithms (Farris 1970), using the Hennig86 program Version 1.5 (Farris 1988) on a Dell Omniplex 466 system. The results were expressed as Nelson consensuses of multiple equally parsimonious, minimum length Wagner trees, obtained by using the mhennig* option with extended branch swapping (bb*) with and without successive approximations to character weighting (xs w; cc;) until stable solutions were reached (Farris 1988), in tandem with the CLADOS program (Nixon 1991). The CLADOS program was useful for 1) obtaining definitions of nodes based on transformation series changes for characters at each given node, 2) carrying out manual branch swapping to further minimize Nelson consensus tree lengths, and 3) illustration. The trees obtained were the most parsimonious explanations of the distribution of the observed data set that could be found, barring use of the Hennig86 ie* option (Farris 1988), which was found impractical (see below). After

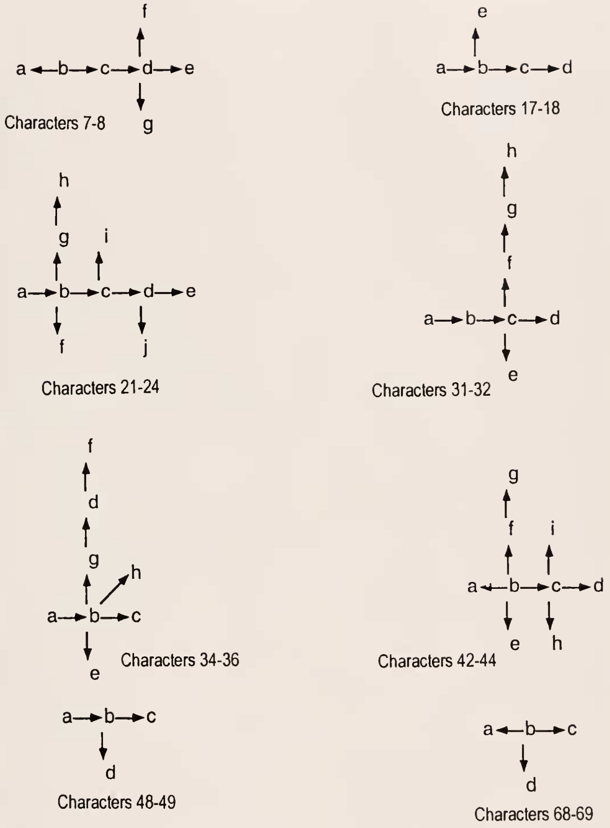

Fig. 1. Diagrams of reticulate transformation series.

Table 1. Matrix of *Aleiodes* species and character states. See Appendix for complete species names and text for explanation of characters.

	0 1 2 3 4 5 6 7
ANCESTOR	0000000111000000000000100010000010010000001110000000010000010000000100000
ABDOMINA	0211020311010000130002100011101132110001002110000021121000101000221100000
ACICULAT	0111010311000000010001000111000121010000001210020021011000001000210100000
AESTUOSU	0211120311010002130012100010001212110001002110001121023000001000211100100
AGILIS	0111120311000002130013100110001211110001002110001121123000001000110000100
ALBITIBI	0111011311000000110002110011000111110000001110000011011010001000210100000
ALBOANNU	0111120301010000030002100111?01131110111002110001021121000101000210101000
ALUTACEU	0111120311000000030001200111000111110010101110000021010000000000110100000
ALIGARHE	0111001211000000010001100011000111010000001110100011011000001000220100000
ALTERNAT	0111010311000000010001000111000121110000001210010021011000001000221100000
ANGUSTAT	0121011211100000010001000111000121110000001210010000?1010000001000210101000
ANNULATU	0101010211000?00030001100111000111010000001110000021010000001000?10100000
ANTENNAT	0111120311000010130002100010001111110111003110000021101000001000210100000
APICALIS	0211020311010000130012100011101132110001002110000021121000101000221100000
ARCTICUS	0111010311000000010001100011000111100000001310030021011010002000210100000
ARIZONIE	0211120311100010030002100010011111210010003110000021111000002000221100000
ARMATUS	0111011211000000010001100011001111110000001210000021010000001000210100000
ARNOLDI	0111120311010000130012100111?01131110001002110000021022000001000210101000
ARSENJEV	0111120311010010030002100010011111110111103110000020001000001000?10100000
ATRICEPS	0211020311010000130002100011101132110001002110000021122000001000221100000
ATRICORN	0111120311010000030012100111001141110001002110002021112000001000210101000
AUTOGRAP	0111011211000000010001100011000111110000001110000011011000011000210100000
BAKERI	1111011211010000020001100111000111110000001110000000?1011000001000210100000
BICOLOR	0111010311000000010001000111000121100000001310010021011010001000210100000
BOREALIS	0111011211000000010001100011000111110000001110000011011000011000210100000
BRETHESI	0211020311010000130002100011101132110001002110000021131000001000221100000
BREVIPEN	0111010311001?00030101300111000110100000111110000020000000000100110100000
BREVIRAD	0111020311010000030001000111001121100000001210000021001?00001000?10100000
BUOCULUS	0111011211000010010001100011000111110000001110000011011000001001210100000
BURRUS	0111120311010000130013100111001131100001002110001021122000001000210101000
CAMERONI	0211120301010010030012100010011111210000003110000021011000002000221100000
CANTHARI	0111011211000000010001100011000111110000001110000001101?000011001?10100000
CARINATU	0111120311010000130013100111001131110001002110001021112000001000221101000
CARINIVE	0211120311010000130013100011001131110001002120000021122010001000221100000
CAUCASIC	0111121311000000130012100011011131100001002110000021001000001000 2??100000
CAZIERI	0211120311110010030002100010001131210000002110000021111000002000221100000
CHLOROTI	0111111301000010010002100110 0?0111210000003110000021110000001001110100000
CIRCUMSC	0111011211000000010001100011000111110000001110000011011000011000210100000
COMPRESS	0221001211100000010001100011000111110000001110100011011000001000220100010
CONFORMI	0111120311010000130013100111001131110001002110001021122000001000210101000
CONVEXUS	0211020311010000130002100011101212110001002110000021121010001000221100001
COXALIS	0111010311000000010001000111000121100000001310010021011010001000210100000
COXATOR	0211010311010000010001000111000121100000001210010021011000001000221100000
CRASSIPE	01010113111?0000010001100111000111110000001110010000?1011000001000?10100000
CRUENTIS	0211120311010000130013100110001311120001002120001021122000001000221101100
CURTISPI	0111010311000000010001200111000111110000001110000021011100000000?10100000
DENDROLI	0111011211000010010001100010000111110000001110000011011010001000210100000
DESERTUS	0111120311000002130012100110001211110001002110001 1?1?23000001001121000100
DISPAR	0111020311001000030101300111001111111001011110000021000000000100110100000
DISSECTO	0211120311010000130012100010001311120001002120001021122010001000221101100
DIVERSIC	01110103110?1000030001200111000121010010101110000021101000000100110100000
DIVERSUS	021112031101000013001210001 0?01211110001002120001021022011001000221101100
DUCTOR	0211020311010000130002100011101132110001002110000021121000101000221100000
EARINOS	0111121311000010030012100110011131210000003110000021101000002000220100000
ECUADORI	0111120311010000030014100111001131110011002110000021102000001000210101000
EURINUS	0111120311010000130013100111001131110001002110001021122000101000210101000
EXCAVATU	0111010311001000030101300111001121110000111211030020000000001100110100000
FAHRINGE	0111020311010002130012100010001212110001002110002021123000001000210001100
FEMORATU	1111010211000000030001100111000111010000001110000011010000001000210100000
FERRUGIL	0111020311000000130012100111001141110001002110000021121000001000210001000
FLAVIDUS	01111213011?0010030002100020001131210000003110000021111000001000211100000
FLAVISTI	0211020321010001130012100000011011130001002110002021132110001000221101100

Table 1. Continued.

	0 1 2 3 4 5 6 7
FLAVITAR	0111020311010000030002100011101112110001002100000021111000001000221100000
FORTIPES	01111213110?0000030012100011011131110000003110000021011000002000210100000
FORTIS	0111120311010000130013100111001131110001002110001021122000001000210101000
FUSCIPEN	0111021311000000010002110011000111110000001110000?1021000001000?10100000
GASTERAT	0211120311010000130013100111001131110001002110001021122000101000211101000
GASTRITO	0111011211000100010001100011000111110000001110000011011000001001110100000
GEOMETRA	0211121301000010030012100010011111210000003110000021011000002000221100000
GLABER	0121?20311010012130012100110001211120001002100001121023000002000110000100
GOSSYPII	0111011211000000010001100011000111110000001110000011011000001000210100000
GRANDIS	0211120311010000030011000011101121100001002110000021111010001000221100000
GRANULAT	0111010311001000010001100111000111010000101210020011010000001100210100000
GRAPHICU	0111110311000010111002100001000101110000101110000021021000001000210100000
GRASSATO	01111203110100001300131001110011311100010021100000211210000010?0210101000
GRESSITT	0111001011000000010011100011000111111000001110000011012000001000210100000
HARRIMAN	0111020311010000130012100110001131110001002100001021121000101000210101000
HELLENIC	011101131100000001000100011100112111000000121?02002101000000000?10100000
HIRTUS	0211020311010000130012100111001131110001002110001021121000101000210101000
INCERTOI	011101031100000001000100011100012110000000121002007101100000100021010000
INCERTUS	0111010311000000010001000111000121110000001210010021111000001000210000000
INDESCRE	0211011311000010010001100011000111110000001110000011011000001000221100000
JAKOWLEW	0111010311100000010001000111000121100010001310030021111000011000?10100000
JAROSLAW	0211120311010000130012100011?00131110001002110000020121000101000221101000
KRULIKOW	0111020311010002130013100110001131120001002120001021103000101000210101100
KUZTLIZK	1111011211000000010001100111000112110000001210000011010000011000210100000
LAPHYGMA	0111011211000000010001100011000111110000001110000011011000001001210100000
LONGICOR	?1110103111?0000030101200111000111010010001110000021110000000100??0100000
LONGIPEN	0111010311101000030101300111000120100000101211000020000000000100110100000
LUCIDUS	0211020321010001130012100000001101140001002100002031232110001000221201100
LYMANTRI	0211011211000010010001100010001111210000001110000011011000011000221100000
MALACOSO	0111011211000000010001100011000111110000001110000011011000001001110100000
MANDIBUL	0211120311010002130012100110001211110001002110002021123000001000221101100
MEDIANUS	0221020311010000030002100111001111110000002110000?1021000001000221101000
MELANOPT	0211020321010001130012100000001101140001002100002021232110001000221201100
MEXICANU	0211020311010001130012100000001101130001002110002021132000001000221101100
MICROCUL	0111120311010000030003100111??0310120001102110000021101010001000221101100
MINIATUS	0121120311010001130013101111001311120000002120002021123000001000210001100
MODESTUS	0111010311000000010012100110000111120000002120001021022000001000210101000
MOLDAVIC	0101010311000000010001000111001121100000001310020021011000001000?10100000
MOLESTUS	0211020311010000130002100111101132110001002110000021121000001000221100000
MORIO	0111120311010000130012100111001311110001002110000021121010001000221101000
NARANGAE	0111010211001?00010001000011000111110000001210020011000000000100110100000
NEGATIVU	0211010311000000010001000110001121110001101210000021110000001000221101000
NEOTROPI	?1110113111?00000100011000110001111100000011100000210110000010?0?10100000
NIGRIBAS	1111011211100010020001100111000111110000001110000?111000000100021010000 0
NIGRICOR	0111011211000000010001100011000111110000001110000011011000011000110100000
NIGRISTE	1111010211000000020001100111000111010000001110000011010000001000210100000
NOCTURNU	0121001211000010010011100010000111110000001110000?1011000001001210100000
NOLOPHAN	0111011211000000010001100011000111110000001110000011011000001001110100000
NOTOZOPH	0211121301000010030002100010011131210000003110000021011000002000221100000
NUNBERGI	0111010311000000010001100111000121100000101310010021011010001000210100000
PALLESCE	0111011211000100010001100011000111110000001110000011011000001001110100000
PALLIDAT	0211011211000000010001100111000111000000001110000011011000001000211100000
PALLIDIS	0111120311010000130003100111001131110001002110001021112000000000210101000
PALMATUS	0121001211100000010001100011000111110000001110100011011000001000220100010
PARASITI	0211020311010000130002100111101132110001002110000021121000001000221100000
PEDALIS	011112130110001003000210002 00?1131210000003110000021111000001000211100000
PELLUCEN	0111001211000000010001100010000111110000001110000011011000001000210100000
PERCURRE	1111011211000?00010001100011000111110000001110000011010000001001210100000
PERINETE	0111010311001000030001200111000121010000001110000021000000000000110100000
PERISCEL	0211020311000000130012100011001311120000002120001021122010001000211101000
PERPLEXU	0111011211000000010001100011000111110000001110000011011000001001210100000
PICTUS	0111011211000000010001100011000111110000001110000011011000011000210100000
PLATYPTE	0111011211000000010001100011000111110000001110000011011000001001210100000

Table 1. Continued.

	0 1 2 3 4 5 6 7
PLEURILI	01110103110100000301010001110001210100000001210000021001000000000110100000
POLITICE	0211120311010001130012100000001101130001002110002021122000001000221101100
PRAETOR	0111110311000010111012100011000111110000101110000021021000001000210100000
PROCERUS	0111010311101000010?0110001100112111000000011100100?1011000001000210100000
PULCHRIP	021112031101001003001211001000113111000000021100000210110000002000221100000
PUNCTIPE	0111010311000?000100011001110001111100000001110000021011000001000110100000
QUADRUM	02111203111110000130012100111001211110001002110?0102112200000010?0221101000
QUEBECEN	02111203010100100100121000100011312101100031100000210110000002000221100000
RILEYI	02111203110100000100121000111011311100000002110000021111000001000221100000
ROGEZENS	011101031110000003010120111100011101001000111000002011000000100?10100000
ROSSI	0211121301000010030012100010011111210000003110000021011000002000221100000
ROSSICUS	01010012110000000100011000110001111100000001110000011011000001000210100000
RUFICEPS	0111121311010001130012100101001211110001002110000021122000001000210101000
RUFICORN	0111120311010000130013100111001131110001002110000021122000101000210101000
RUFIPES	0111120311010000130002100111001131110001002110001021122000001000211101000
RUGOSICO	0111010311001000030101300111001110110000111111000020000000000100110100000
RUGULOSU	0211120311010000130012100111001311110001002120001021121010001000221100100
SANCTIHY	0111010312000000010001000111000121100000101310010021011001001000210100000
SANCTIVE	1111000211100000010001100111001111110000000111000001000000000000210100000
SATANAS	0111010311000000010001000111001121110000000121001 00?1011011001000210100000
SCHIRJAE	0111020311 0?0000130002100111001131110001002110000021121000001000210101000
SCRIPTUS	111101021100000001000110011100111101000000011100000210100000001000?10100000
SCRUTATO	01110112110000000100011000110001111100000001110000011011000011000210100000
SERIATUS	111101021100000003000110011100011111000000011100000110100000001000210100000
SHESTAKO	0211120301010000130002100110001312120001102120000021122110001000221101100
SIBIRICU	0211020311010000130002100111001131110001002110000021121000001000221100000
SIGNATUS	0111010311000000010001000111000121100000001110010021011001101000211100000
SIMILIS	01110112110000000100011000110001111100000001110000011011000011000210100000
SIMILLIM	011101121100001001000110001000011111000000011100000110100000001001210100000
STIGMATO	02110112110001000100011000110001111100000001110000011011000000100111110000
SUDATORI	01110103110000000100011001110001111100000001110000021011000001000?10100000
TATIANAE	0111020311101000030101300111000121110010111 31?030020000010001100110100000
TESTACEU	011100121100010001000110001100111111000000011100000110110000001001210100000
TERMINAL	0111020311010000130012100111001131110001002110000021121000101000210101000
TETRASPH	01110103110000000100010000110001211000000001310040021011000001000210100000
TEXANUS	0111110411000010111002100001000101110000101110000021021000001000210100000
TRANSVER	01110203111100003000120011100012101000000011100000211110000000100??0100000
TRISTIS	0211010311000000010001000111000121110000000121001 00?1011010001000211100000
TURKESTA	0111120311 0?0000130013100111001131110001002100000021122000101000210101000
UFEI	011112031111000013001210011100121111000100211010 10?1122000101000210101010
UNGULARI	02110103110100000100021000110001211000000002110000021021000001000211101000
UNIPUNCT	0111020311010000130012100110001131110001002100000021122000101000210101000
VAUGHANI	0211020301010010030012100010001131210000003110000021011000002000221100000
VENUSTUL	0111020311 0?0001130012100011001211120001002120000021122000001000210101100
WADAI	0111120301010002130002100111001211120001002120001021122000001000210101100
XANTHUS	01110?121100001001000110001100111111000000011100000110110000001001?10100000
NEW SP.1	01110112111010000100013001110001110100000001210020011010000000100210100000
NEW SP.2	0111010312000000010001000111000121100000101310010011011001001000210000000
NEW SP.3	01110112110000000100011000110001111100000001110000021011000001001110100000
NEW SP.4	0111120311010000130013100111001131110001002110001021122000001000221101000
NEW SP.5	01110103110100000100010001110001111100000001210000011011000001000210100000
NEW SP.6	0111120311010000130013100111001131110001002110001021022000001000221101000
NEW SP.7	01110112110100000100010001110001111100000001110000011011000001000210100000
NEW SP.8	0111110311000010111001100011000111110000101110000021011000001000210100000
NEW SP.9	011101121110000001000110001100111111000000011100000110100000001000210100000
NEW SP10	01110103110000000100010001110001211100000001210010021011000001000210100000
NEW SP11	01110103110000000100010001110001211000000001310010021011010001000210100000
NEW SP12	01110112111010100100011001100001111100000001210010011011000001000210100000
NEW SP13	02110103110000000100010001110001211000000001310010021011010001000210100000
NEW SP14	0111010311000000010001100011000111100000101310030021011010001000210100000
NEW SP15	01110012110001000100011000110001111100000001210000011011000001011210100000
NEW SP16	022100101100000001000110001100011111000001010000011011000001000111110000
NEW SP17	0111010311000000010001100011000111100000101310030021011010001000210100000

Table 1. Continued.

	0 1 2 3 4 5 6 7
NEW SP18	0211011211000010010001100010000111110000001110000011011000002000221100000
NEW SP19	0111001211000000010001100011000111110000001110000011011000001011210100000
NEW SP20	0111120311010000130013100111001131110001002110001021122000001000210101000
NEW SP21	0111020311000002130012100010001211110001002100001121023000001000210000100
NEW SP22	0211120311010002130012100100001311110001002110001021133000001000221101100
NEW SP23	0211120311010000130012100110001211110001002110001021123000001000221001100
NEW SP24	0111011211100000010001100011000111010000000110110011011000001000220100010
NEW SP25	0111020311010000130012100110001131110001002110001021121000101000210101000
NEW SP26	0211010312000000010001000111000121110000101210010021011000001000221100000
NEW SP27	0111010311001000010001000111000121100000001310010021011000001000210100000
NEW SP28	0111120311010000030014100111000131110011002110000021112000001000210101000
NEW SP29	0111110411000000111002100001000101110000101110000021021000001000210100000
NEW SP30	1111011211000000030001100111000111010000001110000011010000001000210100000
NEW SP31	0111120311010000130012100111001131110001002110001021122000001000210101000
NEW SP32	0111011211000000010001100011000111110000001110001011011000001001210101000
NEW SP33	1111011211000000020001100111000111010000001110000?101000000100021010000 0
NEW SP34	0211010311000000010001000111000121100000001210010021111000001000221100000
NEW SP35	0111001211000000010001100011000111110000001110000011011000001011210100000
NEW SP36	0101010311000000010001000111000121100000001210000021011000001000210100000
NEW SP37	0211010311000010010001100111001111110000001110000?101100000100022110000 0
NEW SP38	0111011210100010010001100011001111110000001110000011011000011000210100000

the analysis exceeded 128 taxa, a comprehensive matrix (Table 1) was maintained from which 'sample matrices' were drawn for analysis of newly analyzed species within the context of a representative sampling of species analyzed to date.

'Species-group' definition refinement.—It was found that "species-groups" consistently clustered on cladograms derived from Nelson consensuses throughout the course of the study (see Results). Refinement of these species-group definitions was aided by use of sample matrices as follows. For a given species-group, all species previously found to be in the group were included in a sample matrix as described above, as well as most or all species in contiguous species-groups. Manual branch swapping was applied to the Nelson consensus tree after running the matrix on Hennig86 (m*; bb*; xs w; cc) in order to further refine the definition of the species-group by further reducing the length of the tree.

After definitions of all characters, character states, transformation series, and species-groups had been finalized, a final matrix with an approximately equal percentage of species from each species-group (about 61.5%) was analyzed using the mhennig*; option of the Hennig86 program, in order to find the most parsimonious tree (Farris 1988). This percentage was found to meet the requirement of obtaining the tree with 128 taxa, with taxa most evenly distributed across it with respect to species-groups.

Host association analysis.—After a cladogram had been generated as described above, host associations were mapped onto the cladogram. Based on available literature (Shenefelt 1975, Achterberg 1985, Marsh 1979, Shaw 1983, 1994; Shaw 1995, Shaw *et al.* 1997), and museum specimens with host information attached were examined (Rocky Mountain Systematic Entomology Museum, Laramie, WY and Canadian National Collection, Ottawa, ON), host associations were assigned.

CHARACTER SUMMARY

Following is a list describing characters and evolutionary transformation series of those characters in this analysis, along with explanations of how polarities were hypothesized for each transformation series. The number assigned to each character identifies it on the matrix and on the cladogram illustrated by CLADOS. The numbers in brackets indicate character states within the transformation series for a given character, and also appear underneath the numbers assigned to the respective characters in the matrix, and on the CLADOS-generated cladograms for each species-group. Squares on cladogram branches below designated character numbers represent character state transformations which help define the node or species following the squares. If the square is darkened, the square represents an increase in character state number; if white, a reversal is indicated. Unless otherwise stated, the [0] state was that hypothesized to be ancestral based on *Clinocentrus, Rogas* and *Stiropius* specimens examined.

I. *Head Characters*

4. *Shape of 15th flagellomere from base, females*: [0] width/length less than 0.83; [1] compact: width/length greater than 0.83. State [1] was found only in some *Aleiodes* species. Thus, state [0] was hypothesized to be the ancestral state.

6. *Occipital carina*: [0] strong, complete medially; [1] weak or effaced medially. State [1] was found in most *Stiropius* and no *Clinocentrus* or *Rogas* examined, and was hypothesized to be ancestral. This hypothesis was tested by comparing relative parsimony with respect to character polarization. The same matrix was run on Hennig86 as described above for two runs except that polarization was switched for each. Since the alternate polarity was most parsimonious (strong, complete occipital carina ancestral), this alternate hypothesis was accepted; the *Rogas/Clinocentrus* condition was hypothesized to be ancestral.

13. *Flagellum, female*: [0] > 33 flagellomeres; [1] ≤ 33 flagellomeres. All *Stiropius* species examined expressed state [1], and no *Clinocentrus* or *Rogas* species did. The more parsimonious character polarization was found by running each of the two possibilities on Hennig86. Based on parsimony, the reduced number of flagellomeres was hypothesized to be derived where it occurred in *Aleiodes*.

14. *Ocellar diameter/distance between lateral ocellus and compound eye*: [0] < 2.5; [1] ≥ 2.5 (Shaw *et al.* 1997, Figs. 1–5). State [1] was observed in all *Rogas* species examined, and no *Stiropius*. A comparison of parsimony in which the polarity of this character was switched between two otherwise identical matrices showed that the polarization used here was most parsimonious. Thus, state [0] was hypothesized to be the ancestral state.

15. *Ratio of clypeo-antennal space to width of oral space*: [0] greater than 0.82; [1] 0.69–0.82; [2] less than 0.69. Since states [1] and [2] were not found in non-*Aleiodes* species examined, state [0] was hypothesized to be ancestral.

20. *Occipital carina at hypostomal carina*: [0] complete or nearly so; [1] incomplete, effaced well before reaching hypostomal carina. Determining polarity was problematic, since of four *Rogas* species examined, two expressed state [0], and two expressed [1]. The *Clinocentrus* species examined (four unnamed morphospecies) consistently exhibited state [0]. Two *Stiropius* species examined consistently possessed state [1]. Both codings were tried for the ancestor, with no change in the consistency index (c.i.). The above polarization represents the most parsimonious solution. Thus, state [0] was hypothesized to be the ancestral state.

27. *Ratio of malar space to mandibular basal width*: [0] less than 1; [1] greater than or equal to 1. State [0] was found in all *Rogas* and *Clinocentrus* species examined. State [1] was observed in all *Stiropius* examined. A comparison of parsimony between alternate polarizations revealed that the polarization presented here is the simplest explanation.

31. *Vertex sculpturing (path a–d)*: [0] coarsely granulate; [1] smooth, granulate, or faintly rugulose (Shaw *et al.* 1997, Fig. 6); [2] smooth with shallow, dense punc-

tation; [3] shiny, coarsely and densely punctate.

32. *Vertex sculpturing (path e–h)*: [0] nitid; [1] one of conditions in #31; [2] with strong laterally running ridges, or rugose; [3] with fine laterally running ridges (generalized advanced condition; Shaw *et al.* 1997, Fig. 5); [4] finely rugulose. The reticulate character described by the above 2 paths is hypothesized as follows: a = 31[0]; b = 31[1]; c = 31[2]; d = 31[3]; e = 32[0]; f = 32[2]; g = 32[3]; h = 32[04].

	a	b	c	d	e	f	g	h	path
n	0	1	2	3	1	1	1	1	a-d (#31)
n + 1	1	1	1	1	0	2	3	4	e-h (#32)

The above phylogenetic hypothesis is illustrated in Fig. 1d. *Stiropius* species observed all expressed state (a), and *Rogas* species all expressed state (e). A comparison of parsimony between alternate polarizations revealed that the polarization presented here is the simplest explanation.

33. *Medial carina extending down frons*: [0] absent; [1] present, extending less than 0.55 of distance from line between bases of scapes to clypeus; [2] present, extending 0.55 or more of distance from line between bases of scapes to clypeus. States [1] and [2] were observed in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

38. *Lightness of midsection of antennae*: [0] not lighter than both basal and apical sections; [1] lighter than both basal and apical sections (Shaw *et al.* 1997, Fig. 23). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

48. *Clypeal carina (path a–c)*: [0] absent; [1] present, not shelflike; [2] shelflike.

49. *Clypeal carina (path b–d)*: [0] clypeus either not elongate, or with a carina; [1] elongate clypeus without carina. The reticulate character described by the above 2 paths is hypothesized as follows: a = 49[0]; b = 49[1]; c = 49[2]; d = 50[1]

	a	b	c	d	path
n	0	1	2	1	a-c (#48)
n + 1	0	0	0	1	b-d (#49)

The above phylogenetic hypothesis is illustrated in Fig. 1g. States [1] and [2] were observed in no non-*Aleiodes* examined. Thus, state [0] was hypothesized to be the ancestral state.

51. *Length of first flagellomere*: [0] ≥ scape length; [1] < scape length. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

54. *Clypeus height divided by width*: [0] > 0.65; [1] ≤ 0.65 ≥ 0.42; [2] < .42 > .30; [3] ≤ 0.30. Height was defined as distance between clypeo-labral suture and dorsal edge of clypeus. Width was defined as distance between inner edges of tentorial pits. All *Stiropius* and *Rogas* examined expressed state [0]. *Clinocentrus* expressed state [1]; However, given that *Stiropius* and *Rogas* are phylogenetically closer to *Aleiodes* than *Clinocentrus* (Whitfield 1992), the elongated clypeal condition in *Clinocentrus* was hypothesized to be independently derived with respect to the *Aleiodes* condition, and state [0] was hypothesized to be ancestral.

55. *Third maxillary palpomere*: [0] not swollen; [1] swollen. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

69. *Clypeus shape*: [0] not abruptly edged, not flat ventrad (ancestor); [1] abruptly edged, flat ventrad. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

70. *Wide, flat flange on lower side of mandible*: [0] not strongly present; [1] strongly present. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

II. *Mesosomal Characters*

3. *Median carina of propodeum*: [0] short and forking before halfway point of propodeum (Achterberg 1991, Fig. 121); [1] not forking before halfway point of propodeum. *Rogas* and *Clinocentrus* species examined expressed the [0] state. *Stiropius* and *Aleiodes* independently expressed different states which were not [0]. Thus, state [1] was hypothesized to be the ancestral state for *Aleiodes.*

7. *Sculpture of propodeum antero-laterally (path a–e)*: [0] finely, smoothly granulate; [1] coarsely granulate, or areolate; [2] rugulocostate over granulate surface, not shiny; [3] rugose over granulate surface or no underlying granulation; [4] smooth-punctate.

8. *Sculpture of propodeum antero-laterally (path f–g)*: [0] granulate with faint rugulosity or granulate (Shaw *et al.* 1997, Figs. 7–10); [1] one of states in #7; [2] nitid. The above two paths constitute a reticulate transformation series, which is hypothesized as follows: a = 7[0]; b = 7[1]; c = 7[2]; d = 7[3]; e = 7[4]; f = 8[0]; g = 8[2]

	a	b	c	d	e	f	g	path
n	0	1	2	3	4	3	3	a-e (#7)
n + 1	1	1	1	1	1	2	0	f-g (#8)

The above phylogenetic hypothesis is illustrated in Fig. 1a. The states represented by (b) were not found in *Aleiodes.* The propodeums of *Clinocentrus* and *Rogas* were areolate; that of *Stiropius* was coarsely granulate. Thus, one of the states represented by (b) was hypothesized to be the ancestral state.

12. *Pronotum angle*: [0] not shelflike (Achterberg 1991, Figs. 283, 294, 380); [1] shelflike (Achterberg and Penteado-Dias 1995, Figs. 6, 11, 16, 21, 26) State [1] was not observed in any non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

16. *Large setal pits on scutellum*: [0] absent; [1] present. Since state [1] was not found in any non-*Aleiodes* species examined, state [0] was hypothesized to be ancestral.

19. *Prescutellar carina*: [0] without an anterior invagination; [1] with an anterior invagination. State [1] was observed in no non-*Aleiodes* species. Thus, state [0] was hypothesized to be the ancestral state.

21. *Mesopleuron central disc sculpturing (path a–e)*: [0] shiny coarse granulation; [1] granulate; [2] smooth-punctate; [3] heavily punctate.

22. *Mesopleuron central disc sculpturing (path f–h)*: [0] coarsely rugulose; [1] granulate, or other states in #21; [2] costate from granulate or partly costate, partly granulate; [3] partly smooth, partly rugulose.

23. *Mesopleuron central disc sculpturing (c–i)*: [0] not nitid; [1] nitid.

24. *Mesopleuron central disc sculpturing (d–j)*: [0] not costate from punctate; [1] costate from punctate. The reticulate character described by the above 4 paths is hypothesized as follows: a = 21[0]; b = 21[1]; c = 21[2]; d = 21[2]; e = 21[4]; f = 22[0]; g = 22[2]; h = 22[3]; i = 23[0]; j = 24[1].

	a	b	c	d	e	f	g	h	i	j	path
n	0	1	2	3	4	1	1	1	2	3	a-e(#21)
n+1	1	1	1	1	1	0	2	3	1	1	f-h(#22)
n+2	1	1	1	1	1	1	1	1	0	1	c-i(#23)
n+3	0	0	0	0	0	0	0	0	0	1	d-j(#24)

The above phylogenetic hypothesis is illustrated in Fig. 1c. In this case, a reticulate transformation series was considered the best way to interpret the data because of the high degree of variability. No *Aleiodes* species were coded with (a). *Clinocentrus* and *Rogas* species examined expressed the nitid condition, and *Stiropius* expressed shiny, coarse granulation. Given the plasticity of mesopleural sculpturing within genus *Aleiodes,* as can be seen by the above complex reticulation of character states, the *Aleiodes* nitid condition was hypothesized to have evolved independently from the *Rogas* nitid condition. The shiny coarse (a) condition was hypothesized to have been the ancestral condition for *Aleiodes.*

25. *Sternaulus*: [0] not sculptured; [1] rugose or rugulose. *Stiropius* expressed state [0]. *Rogas* expressed a uniquely foveate condition not found anywhere else, and *Clinocentrus* expressed rugation less regular than the *Rogas* condition, but more so than the condition observed in *Aleiodes.* Since only *Aleiodes* species expressed the [0] condition in common with *Stiropius,* the [0] condition was hypothesized to be ancestral.

39. *Mesopleural pit posteriad to central disc of mesopleuron*: [0] absent; [1] present. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

40. *Protuberances or a raised ridge immediately anteriad to propodeal apex*: [0] absent; [1] present. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

41. *Pronotal anterior flange*: [0] < 0.28 of pronotal length; [1] ≥ 0.28 of pronotal length. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

50. *Postero-dorsal surface of scutum*: [0] mostly nitid, sometimes weakly rugulose; [1] weakly rugulose, not shiny; [2] at least some strong costae; costae smooth; [3] smooth, not nitid. State [0] was observed in *Clinocentrus, Rogas,* and *Stiropius* species examined, but in no *Aleiodes,* and was hypothesized to be the ancestral condition.

52. *Notauli at mid-dorsal surface of scutum*: [0] without carinae or foveae or finely foveate, non-carinate; [1] coarsely foveate, and/or usually carinate posteriad; [2] smooth, not nitid. States [1] and [2] were not found in any *Rogas* or *Stiropius* examined. However, the coarsely foveate condition was ubiquitous in *Clinocentrus.* Given the above, it was hypothesized that state [0] was ancestral, and that the *Clinocentrus* condition was derived in parallel with the state's appearance in *Aleiodes.*

53. *Scutal sculpturing excluding postero-dorsal surface and notauli*: [0] rugulose sculpturing over a nitid surface; [1] granulate; [2] punctate; [3] nitid or smooth, not nitid. States [1], [2], and [3] were not expressed by non-*Aleiodes* species examined. *Stiropius* expressed the coarsely granulate condition, *Rogas* expressed rugulose sculpturing over a nitid surface, and *Clinocentrus* expressed a nitid-punctate scutal surface. Since *Rogas* is considered the sister group of Aleiodes (Whitfield 1992), state [0] was hypothesized to be ancestral.

61. *Propodeum dorsal profile*: [0] rounded; [1] flattened. State [1] was not observed in non-*Aleiodes* species examined. State [0] was hypothesized to be ancestral.

63. *Ratio of pronotal medial length to head length*: [0] ≥ 0.30; [1] < 0.30. Head length was defined as distance from the occipital carina at the vertex to the line between posterior edges of antennal sutures. State [1] was observed in *Stiropius* and some *Aleiodes,* but not in *Rogas* or *Clinocentrus.* Given the very small ocelli of *Stiropius,* such that the ocellocular distance/ocellar diameter ratio was consistently much greater than one, the vertex broad in comparison with the three other genera, and the antennal flagellomeres over twice as long as wide in contrast with the three other genera, it was hypothesized that the *Stiropius* condition was independently derived. Thus, it was hypothesized that state [0] was the ancestral condition.

III. *Metasomal Characters*

2. *Median carina of tergite II*: [0] undifferentiated from other coarse carinae (Achterberg 1991, Fig. 124); [1] differentiated from other carinae (Achterberg 1991, Fig. 377); [2] undifferentiated from other fine carinae. State [0] is the *Stiropius/Rogas* condition. *Clinocentrus* shared [1] with some *Aleiodes.* Since *Clinocentrus* is considered most distantly related to *Aleiodes* of the three outgroup genera (Whitfield

1992), it was hypothesized that state [1] was independently derived in *Clinocentrus* and *Aleiodes*.

5. *Median triangle of tergite II*: [0] absent; [1] small and without well developed anterior carinae (Achterberg 1991, Fig. 290); [2] large and associated with anterior carinae which run laterally nearly to margins of tergite (Achterberg 1991, Fig. 300). The presence of a median triangle differentiates most *Aleiodes* with respect to *Rogas* and *Stiropius*. Thus, state [0] was hypothesized to be the ancestral state.

10. *Length of metasomal tergite I, female*: [0] tergite apical width/tergite length greater than or equal to 0.87 (not elongate); [1] tergite apical width/tergite length less than 0.87 (elongate). An elongate first metasomal tergite was not present in *Stiropius*, and only occasionally present in *Clinocentrus* and *Rogas*. Thus, its occasional presence in *Aleiodes, Clinocentrus, and Rogas* was hypothesized to be independently derived.

28. *Setal mat on metasomal tergites 4–6 of males*: [0] absent; [1] present (Shaw *et al.* 1998, Fig. 1). State [1] was expressed by no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

29. *Medial pits on tergites 4–7, males*: [0] absent; [1] present (Shaw *et al.* 1997, Figs. 13, 15, 17) State [1] was expressed by no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

34. *Sculpturing of metasomal tergite I (path a–c)*: [0] weakly or strongly costate, costae relatively widely spaced, often over weak granulation; [1] rugulocostate or rugocostate; or costate, costae narrowly spaced, no underlying sculpturing; [2] finely rugulose to finely rugulocostate (Shaw *et al.* 1997, Figs. 11, 12).

35. *Sculpturing of metasomal tergite I (path e–f)*: [0] rugose or rugulose; [1] one of conditions of #34; [2] smoothly rugose; [3] strongly costate, costae narrowly spaced, no underlying sculpturing; [4] weakly costate, costae narrowly spaced, no underlying sculpturing, or nitid.

36. *Sculpturing of metasomal tergite I (path b–h)*: [0] not smoothly, finely granulate; [1] smoothly, finely granulate. The reticulate character described by the above two paths is hypothesized as follows: a = 34[0]; b = 34[1]; c = 34[2]; d = 35[3]; e = 35[0]; f = 35[4]; g = 35[2]; h = 36[1].

	a	b	c	d	e	f	g	h	path
n	0	1	2	1	1	1	1	1	a-c (#34)
n + 1	1	1	1	3	0	4	2	1	e-f (#35)
n + 2	0	0	0	0	0	0	0	1	b-h (#36)

The above phylogenetic hypothesis is illustrated in Fig. 1e. State (a) was observed in all *Clinocentrus* and *Rogas* examined, and in some *Aleiodes* species. The coarsely granulate *Stiropius* condition was thus hypothesized to be a derived synapomorphy for that group, and (a) was hypothesized to be ancestral.

42. *Metasomal tergite III sculpturing (path a–d)*: [0] completely, finely smooth-aciculate; [1] weakly to strongly rugulocostate or weakly costate over granulate background; costae not smooth, tergite not shiny; [2] smooth-aciculate or smoothly rugulose anteriad, nitid or smooth-punctate posteriad, or entirely nitid or smooth punctate; [3] shallowly rugulose or rugulopunctate anteriad, finely punctate posteriad or completely finely punctate.

43. *Metasomal tergite III sculpturing (path e–g)*: [0] smooth, faintly granulate, shiny; [1] one of states of #42; [2] entirely carinate; [3] strongly rugose.

44. *Metasomal tergite III sculpturing (path h–i)*: [0] completely smooth, shiny, no trace of granulation; [1] one of conditions of #42; [2] densely punctate or rugulopunctate anteriad; shiny posteriad, or entirely densely punctate. The reticulate character described by the above 3 paths is hypothesized as follows: a = 42[0]; b = 42[1]; c = 42[2] d = 42[3]; e = 43[0] f = 43[2]; g = 43[3]; h = 44[0]; i = 44[2].

	a	b	c	d	e	f	g	h	i	path
n	0	1	2	3	1	1	1	2	2	a-d (#42)
n + 1	1	1	1	1	0	2	3	1	1	e-g (#43)
n + 2	1	1	1	1	1	1	1	0	2	h-i (#44)

The ancestral state is (b). The above phylogenetic hypothesis is illustrated in Fig. 1f. Since state (a) was ubiquitous in all *Rogas* species examined and in many *Aleiodes*, it was hypothesized to be ancestral.

45. *Excavated medial areas on metasomal tergites II and III*: [0] absent; [1] present (Achterberg 1985, Fig. 12). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

46. *Apex of abdomen, females*: [0] not compressed; [1] compressed. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

47. *Fourth metasomal tergite (MT IV)*: [0] MT IV unsculptured; [1] MT IV slightly sculptured; [2] MT IV mostly sculptured, not heavily rugulose; [3] MT IV heavily rugulose, but not a complete carapace over apicad tergites; [4] MT IV a heavily rugulose, complete carapace over apicad tergites. States [1] through [4] were found in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

56. *Metasomal dorsum color*: [0] not entirely black; [1] entirely black. State [1] was observed in some unicolored *Stiropius* and *Clinocentrus* species, and in some *Aleiodes* species. Since all *Rogas* species observed were uniformly yellow, and many *Aleiodes* expressing state [1] had heads and/or mesosoma that were not black, it was hypothesized that the *Stiropius* and *Clinocentrus* conditions were independently derived from the condition in *Aleiodes*, and that state [0] was ancestral.

57. *Metapleural pit*: [0] not slightly larger than propodeal spiracle, deep and round; [1] slightly larger than propodeal spiracle, deep and round. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

58. *Head/mesosoma/apical metasomal coloration (metasomal tergite III and posteriad; females)*: [0] not all black with bicolored metasoma; [1] all black with bicolored metasoma. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

59. *Metasomal tergite II coloration*: [0] not consistently black laterally, yellow medially; [1] consistently black laterally, yellow medially. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

62. *Ovipositor length*: [0] less than ½ length of metafemur; [1] greater than or equal to ½ length of metafemur. All *Stiropius* species examined had short ovipositors, and most *Rogas* species and all *Clinocentrus* species examined had long ovipositors. Since most *Aleiodes* species examined had short ovipositors, short ovipositor length was hypothesized to be the ancestral condition.

71. *Lateral edges of metasomal tergite I*: [0] not parallel; [1] parallel. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

72. *Metasomal tergite III*: [0] not carapace-like; [1] carapace-like, extending over apicad tergites. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

IV. *Wing Characters*

9. *Second submarginal cell*: [0] long, narrow, vein 2RS/vein 2-M less than 0.4; 2RS parallel or nearly so with r-m; [1] trapezoidal or rectangular, defining veins often arched, 2RS/2-M greater than 0.45 and less than 0.71; [2] quadrate; 2RS parallel or nearly so with r-m, and 2RS/2-M greater

than 0.71. Since the second submarginal cells of *Clinocentrus, Rogas,* and *Stiropius* species examined all expressed state [1], and since the ordering described above is most logical, it was hypothesized that this is a bipolar character

17. *RS vein of hind wing (path a–d)*: [0] marginal cell widest basally, RS vein not recurved apically (Achterberg 1991, Fig. 54); [1] marginal cell narrowest in middle; RS vein moderately to slightly recurved apically, never nearly touching wing margin (Achterberg 1991, Fig. 278); [2] RS vein parallel with costal wing margin in basal ½–⅔, abruptly angling posteriad apically; [3] marginal cell not narrowest in middle; RS vein not recurved or angling; straight or nearly (Achterberg 1991, Fig. 291).

18. *RS vein of hind wing (path b–e)*: [0] not extremely narrow in middle; vein not nearly touching wing margin; [1] extremely narrow in middle, vein nearly touching wing margin (Achterberg 1993a, plate 31). The reticulate character described by the above two paths is hypothesized as follows: a = 17[0]; b = 17[1]; c = 17[2]; d = 17[3]; e = 18[1].

	a	b	c	d	e	path
n	0	1	2	3	1	a-d (#17)
n + 1	0	0	0	0	1	b-e (#18)

State (a) was observed in *Clinocentrus, Rogas,* and *Stiropius* species examined, but not in any *Aleiodes.* Thus, it was hypothesized to be the ancestral state. State (b) was hypothesized to be the most basal state for this character within *Aleiodes,* since it represents only one modification from the ancestral state: the recurvation of the apical section of the RS vein. States (c) and (d) were hypothesized to represent a progressive straightening of the RS vein from the original curved condition. State (e) was hypothesized to represent a bifurcation in the evolution of this character, such that the (b) condition evolved in some Aleiodes lineages into the straightened (c) and (d) conditions, and on the other hand into the extremely recurved (e) condition in another. The above phylogenetic hypothesis is illustrated in Fig. 1b.

26. *Wing coloration*: [0] fumate; [1] hyaline; [2] patterned. State [1] was universal for all *Clinocentrus, Rogas,* and *Stiropius* species examined, and most *Aleiodes* species. States [0] and [2] were not observed in any non-*Aleiodes* species examined. Given the ubiquity of state [1], were non-hyaline wings to occur in non-*Aleiodes species,* they would almost certainly represent a parallel derived condition. Thus, state [1] was hypothesized to be the ancestral state.

30. *Hindwing vein 1A*: [0] not extending past vein cu-a; [1] extending past vein cu-a. State [1] was found in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

60. *Fore wing width divided by length*: [0] less than 0.29 (long, narrow); [1] 0.29–0.34; [2] greater than or equal to 0.35 (broad). States [0] and [2] were not observed in non-*Aleiodes* species examined. State [1] was hypothesized to be ancestral; thus, the character was hypothesized to be bipolar.

V. *Leg Characters*

0. *Inner apex of hind tibia*: [0] with setae normal and unmodified; [1] with setae flattened coming to a point apically, forming an apical fringe (Achterberg 1991, Fig. 122). State [1] is the norm for *Rogas,* but does not occur in any *Stiropius* or *Clinocentrus* species so far as known (Shaw 1993). It was considered to be derived in *Rogas* and in any *Aleiodes* in which it occurred. Thus, state [0] was hypothesized to be the ancestral state.

1. *Tarsal claw*: [0] either no tarsal teeth or if present, preapical lobe present (Achterberg 1991, Figs. 123, 322); [1] no preapical lobe, with basal tarsal teeth only; [2] no preapical lobe, tarsal teeth extending almost to apical tooth, or tarsi completely pectinate (Fig. 2c; Shaw *et al.* 1997, Figs. 20–22). Since the presence of tarsal teeth with no preapical lobe is an autapomor-

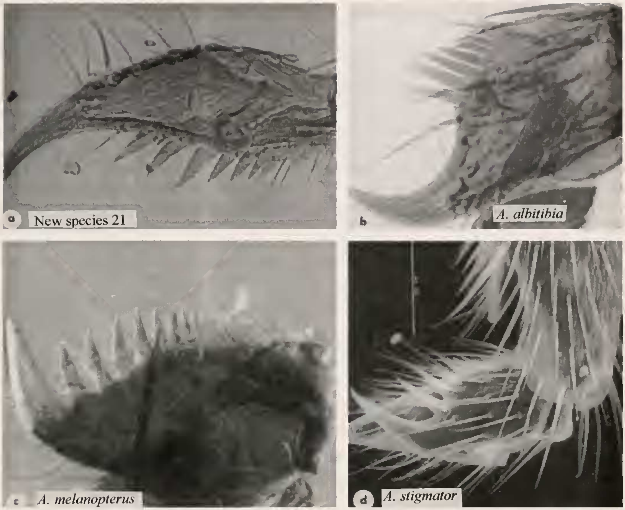

Fig. 2. Tarsal claws. a, "new species 21;" b, *A. albitibia*; c, *A. melanopterus*; d, *A. stigmator*.

phy for genus *Aleiodes* distinguishing it from *Clinocentrus*, *Rogas*, and *Stiropius*, state [0] in part defines the hypothetical ancestor. Thus, state [0] was hypothesized to be the ancestral state for these four genera, and state [1] was hypothesized to be the ancestral state for *Aleiodes*.

11. *Tarsal segment 4, female*: [0] elongate: length ≥ 1.6 times apical width; [1] compact: length < 1.6 times width. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

37. *Lightness of hind tarsus*: [0] not considerably lighter than tibia; [1] considerably lighter than tibia (Shaw *et al.* 1997, Fig. 24). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

64. *Number of tarsal claw teeth*: [0] none; [1] 5 or less; [2] more than 5. State [0] was shared by some *Rogas*, all *Clinocentrus* and *Stiropius*, so far as known, and was hypothesized to be the ancestral state.

65. *Shape of apical tarsal tooth*: [0] not present; [1] incompletely toothed; [2] completely toothed (Fig. 2c; Shaw *et al.* 1997, Figs. 19–22). The incomplete form was reminiscent of a thickened seta, with a hair-like, flexible apex. State [0] was hypothesized to be ancestral, for reasons stated for character 64.

66. *Setae between apical tarsal tooth and claw*: [0] present (Fig. 2a, b); [1] absent (Fig. 2c, d). Several *Aleiodes* species which expressed incompletely toothed apical tarsal teeth, also expressed basal tarsal teeth only. In addition, they expressed a gradation of thickened, prominent setae which became progressively thinner with

increasing apical position apicad of the apical tooth. Thus, it was hypothesized that state [1] represented the completion of a transformation of apical setae into teeth, and thus that state [0] was ancestral.

67. *Shape of apical tarsal claw (path a–c)*: [0] nearly without a hook (Fig. 2a); [1] not abruptly hooked (Fig. 2b); [2] abruptly hooked with straight shank which angles at nearly 90 degrees (Fig. 2c).

68. *Shape of apical tarsal claw (path b–d)*: [0] one of above states; [1] abruptly hooked with straight shank which angles at less than 90 degrees (Fig. 2d). The reticulate character described by the above two paths is hypothesized as follows: a = 67[0]; b = 67[1]; c = 67[2]; d = 68[1].

	a	b	c	d	path
n	0	1	2	1	a-c (#67)
n + 1	0	0	0	1	b-d (#68)

State (b) was universal in all non-*Aleiodes* species examined, and most *Aleiodes* species. Thus, it was hypothesized to be the ancestral state. The above phylogenetic hypothesis is illustrated in Fig. 1h.

RESULTS

Throughout the development of this analysis, species-groups emerged and defined themselves by consistently clustering on the most parsimonious consensus tree. Once all species had been analyzed, 18 well-defined species-groups had emerged. Figs. 6 to 8 show the major species-groups within genus *Aleiodes*. Fig. 5 shows the overall phylogenetic pattern of the genus, with species-groups represented by exemplar species.

Initially assigning equal weight to all characters resulted in one most parsimonious tree using the mhennig* option. This tree had a length of 475 steps, a consistency index (c.i.) of .25, and a retention index (r.i.) of .78. Extended branch swapping (bb* option) resulted in 755 equally parsimonious trees all with lengths of 475 steps.

The final solution for successive iterations to character weighting applied to the trees before the Nelson consensus was run resulted in 755 most parsimonious trees, each with length of 624 steps, a c.i. of .56, and an r.i. of .91. The modified Nelson consensus tree of the final solution for the overall unweighted analysis, after manual branch swapping, is shown in Fig. 5. The Nelson consensus tree length of the unweighted tree loaded into CLADOS was reduced by 140 steps by manual branch swapping.

The genus can be divided into three major sections: basal, intermediate, and derived species. Basal species are defined as those in which 1) the occipital carina is usually weak or effaced medially, 2) hind-wing RS vein is recurved, 3) hind-wing vein 1A usually does not extend past vein cu-a, 4) propodeal sculpturing is coarsely granular, or rugulocostate over a granulate surface, 5) mesopleuron is granulate, 6) mesopleural pit posteriad to mesopleuron central disk is absent, and 7) median triangle of tergite II is small or absent and without well developed anterior carinae. In the overall cladogram (Fig. 3), groups 1–6 are basal groups.

Intermediate species are defined as those with the above characteristics except 1) the occipital carina is complete medially, 2) propodeal sculpturing is rugose, 3) the hind-wing RS vein may be straight, and 4) mesopleuron may be rugulose (groups 7–9).

Derived species are defined as those with the characteristics for intermediate species except 1) mesopleuron sculpturing is smooth punctate or smooth, 2) the hind-wing RS vein is almost always straight, 3) third metasomal tergite is either smooth-aciculate or smoothly rugulose or rugulocostate anteriad and either smooth-shiny or smoothly rugulose posteriad, or entirely smooth or entirely punctate 4) hind-wing vein 1A extends past vein cu-a, and 5) the antero-medial triangle of metasomal tergite II is large and associated with anterior carinae which run laterally. There is an increasing tendency with derived position on the cladogram for the mesopleural pit posteriad to mesopleuron central disk to be present (groups 10–18).

Species-group definitions

Some species in unresolved clusters, or which did not clearly fall within any cluster, were not placed within any species-group. These species either were in the basal section, or fell at the base of a well-defined species-group. Such species were *A. armatus, A. arnoldi, A. cariniventris, A. ferrugileti, A. jaroslawensis, A. medianus, A. modestus, A. pellucens, A. quadrum, A. rossicus, A. ruficeps, A. sibiricus, A. ungularis,* and new species 7 and 9.

Species included below which will be published later by Shaw *et al.* are designated as new species (number). This text does not constitute a publication of any new species.

1. The ***gressitti*** species-group (Fig. 4a) consists of *A. gressitti* (Muesebeck) and new species 16. This is the basal-most group in the genus, and is defined by propodeum and metasomal tergite I finely, smooth-shiny granulate.
2. The ***compressor*** species-group (Fig. 4a) consists of known species *A. aligarhensi* (Quadri), *A. compressor* (Herrich-Schaffer), *A. palmatus* (Walley), and new species 24. The group is monophyletic, and defined by the following synapomorphies: 1) apex of female abdomen compressed, and 2) apical tarsal tooth complete.
3. The ***gastritor*** species-group (Fig. 4b) is a large monophyletic basal group defined by pronotal medial length ≤ .30% of head length. It consists of *A. buoculus* Marsh, *A. cantharius* (Lyle), *A. dendrolimi* (Matsumura), *A. gastritor* (Thunberg), *A. laphygmae* (Viereck), *A. malacosomatos* (Mason), *A. nocturnus* Telenga, *A. nolophanae* (Ashmead), *A. pallescens* Hellen, *A. perplexus* (Gahan), *A. platypterygis* (Ashmead), *A. simillimus* (Ashmead), *A. stigmator* (Say), *A. testaceus* (Telenga), *A. xanthus* (Marshall), and new species 3, 15, 32, and 35.
4. The ***circumscriptus*** species-group (Fig. 6c) is a basal, monophyletic group defined by metasomal tergite II consistently yellow medially and black laterally. Species within the group are: *A. autographae* (Viereck), *A. borealis* Thomson, *A. circumscriptus* (Nees von Esenbeck), *A. nigricornis* Wesmael, *A. pictus* (Herrich-Schaffer), *A. similis* (Curtis), *A. scrutator* (Say), and new species 38.
5. The ***pallidator*** species-group (Fig. 4d), also basal and monophyletic, is defined by eye diameter greater than 2.5× ocellocular space, and tarsal claws pectinate. The species in this group are *A. indiscretus* (Reardon), *A. lymantriae* (Watanabe), *A. martini* Marsh and Shaw, *A. pallidator* (Thunberg) and new species 37.
6. The ***seriatus*** species-group (Marsh *et al.* 1998; Fig. 4e) is basal and monophyletic and is defined by hind tibial apex with flattened setae forming a fringe. The group consists of *A. bakeri* (Brues), *A. femoratus* Cresson, *A. kuslitzkyi* Tobias, *A. nigribasis* (Enderlein), *A. nigristemmaticum* (Enderlein), *A. sanctivincentensis* (Shenefelt), *A. percurrens* (Lyle), *A. scriptus* (Enderlein), *A. seriatus* (Herrich-Schaffer), and new species 30 and 33.
7. The ***procerus*** species-group (Fig. 5a), which is monophyletic, consists of *A. angustatus* (Papp), *A. crassipes* Telenga, *A. granulatus* (De Gant), *A. narangae* (Rohwer), and *A. procerus* Wesmael, and new species 1. It is closely related to the *A. dispar* species-group. The group shares the following synapomorphies: 1) metasomal tergite 4 slightly sculptured, and 2) metasomal tergite 1 elongate. All except *A. crassipes* and *A. angustatus* share a long, shelflike pronotum.

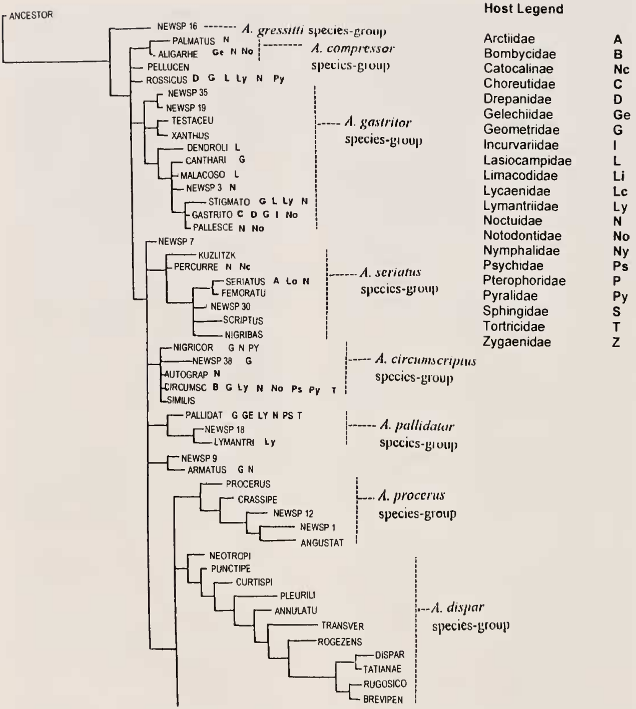

Fig. 3. Cladogram showing overall phylogenetic pattern of *Aleiodes*. Species-groups are represented by exemplar species. Hosts and respective codes are listed in legend. Host associations for *Aleiodes* species are represented by codes next to species.

8. The ***coxalis*** species-group (Fig. 5b) is an intermediate monophyletic group defined by: 1) rugulose to rugose mesopleuron, and 2) vertex with widely separated laterally running ridges. The following species fall in this group: *A. aciculatus* Cresson, *A. alternator* (Nees von Esenbeck), *A. arcticus* Thomson, *A. bicolor* (Spinola), *A. coxalis* (Spinola), *A. coxator* Telenga, *A. hellenicus* Papp, *A. incertoides* Telenga, *A. incertus* Kokoujev, *A. jakolewi* Kokoujev, *A. moldavicus* Tobias, *A. negativus* Tobias, *A. nunbergi* Noskiewicz,

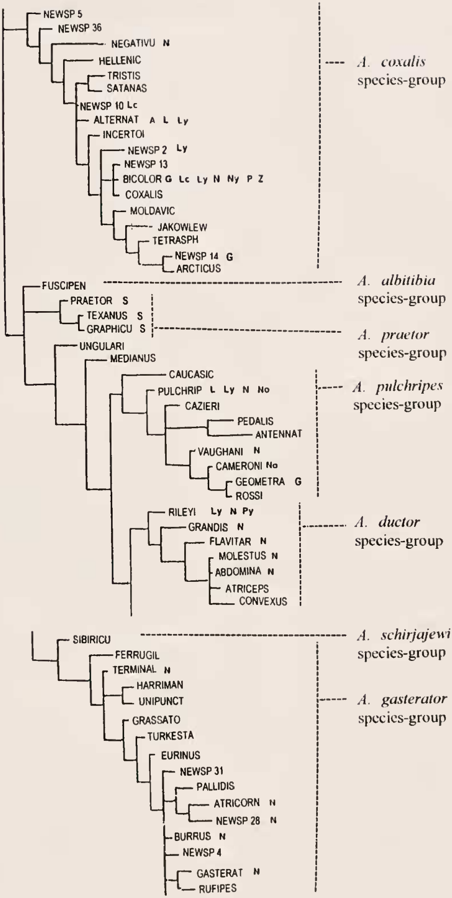

Fig. 3. Continued.

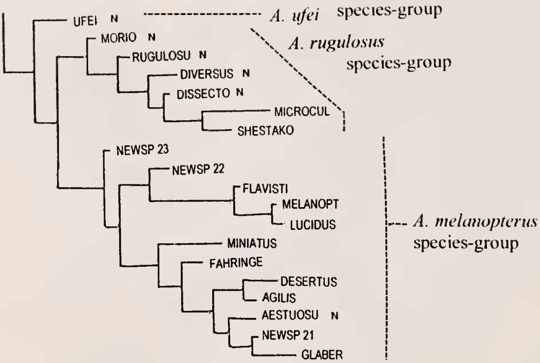

Fig. 3. Continued.

A. sanctihyacinthi (Provancher), *A. satanus* Telenga, *A. signatus* (Nees von Esenbeck), subgenus *Tetrasphaeropyx* Ashmead; *A. tristis* Wesmael, and new species 2, 5, 10, 11, 13, 14, 17, 26, 27, 34, and 36.

9. The ***dispar*** species-group (Fig. 5c), a monophyletic group, consists of *A. aleutaceus* Granger, *A. annulatus* Granger, *A. brevipendulatus* Achterberg, *A. breviradialis* Granger, *A. curtispina* Granger, *A. dispar* (Curtis), *A. diversicornis* Granger, *A. excavatus* (Telenga), *A. longicornis* Granger, *A. longipendulatus* Achterberg, *A. neotropicalis* (Shenefelt), *A. perinetensis* Shenefelt, *A. plurilineatus* (Cameron), *A. punctipes* Thomson, *A. rogezensis* Granger, *A. rugosicostalis* Achterberg, *A. tatianae* (Telenga), and *A. transversestriatus* Granger. It is defined by the narrow forewing, which has a length/widest width ratio ≤ 0.29.
10. The ***albitibia*** species-group (Shaw *et al.* 1998b; Fig. 6b), consisting of *A. albitibia* (Herrich-Schaffer) and *A. fuscipennis* (Szepligeti), is defined by nitid mesopleuron. This character state also occurs in *A. pulchripes* Wesmael, which falls well outside of this group.
11. The ***praetor*** species-group (Shaw *et al.* 1998b; Fig. 6b) is monophyletic and consists of *A. graphicus* (Cresson), *A. praetor* (Reinhard), *A. texanus* Cresson, and new species 8 and 29. The group is defined by: 1) the strongly recurved hindwing radiellen vein which nearly touches the costal margin; 2) lateral ocellar diameter greater than 2.5 times ocellocular distance; and 3) short 15th flagellomere.
12. The ***apicalis*** species-group (Shaw *et al.* 1998a; Fig 6a) is a derived monophyletic group.
13. The ***pulchripes*** species-group (Shaw *et al.* 1997; Fig. 6c) is a derived monophyletic group.
14. The ***gasterator*** species-group (Fig. 7a) is paraphyletic, and it is the basal species-group within the derived species-group cluster of the derived section. This species-group cluster is defined by clypeus abruptly edged, flat ventrad (69[1]), and is composed of the *A.*

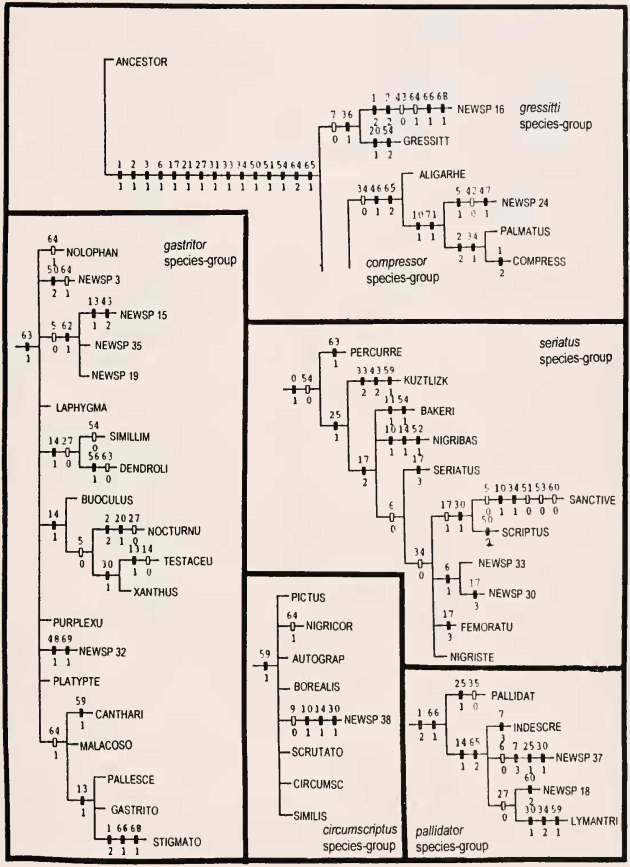

Fig. 4. Species-groups within the basal section of *Aleiodes*. Numbers over boxes represent character numbers; those underneath represent character states of taxa distal of the boxes.

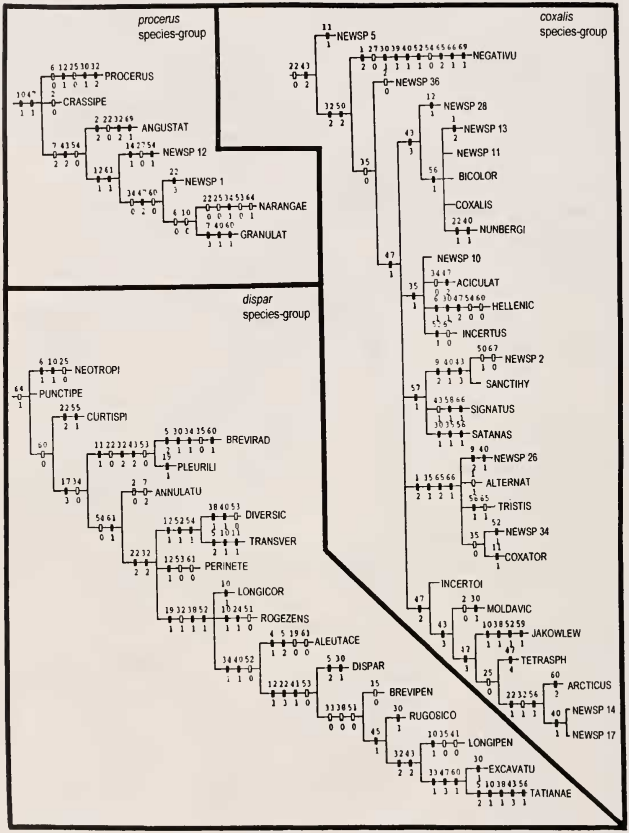

Fig. 5. Species-groups within the intermediate section of *Aleiodes*.

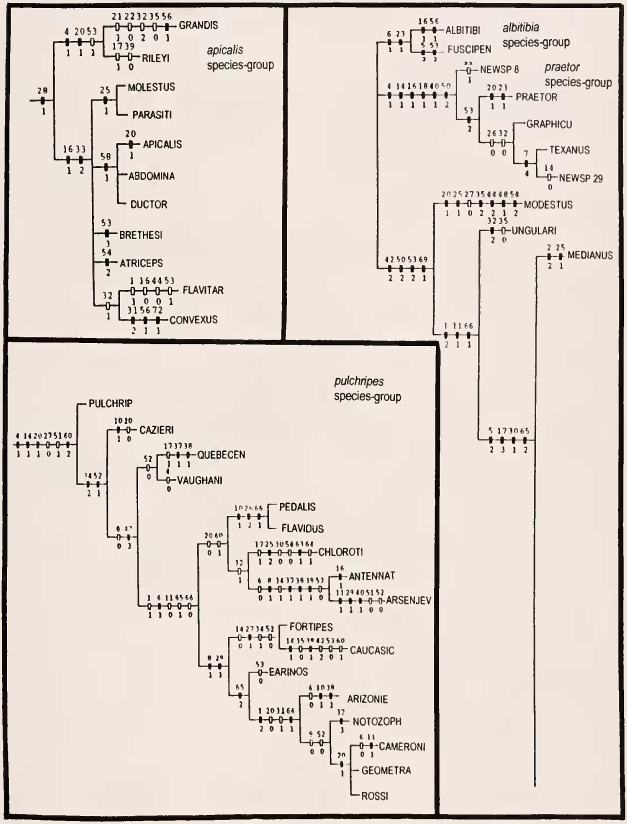

Fig. 6. Species-groups at and near the base of the derived section.

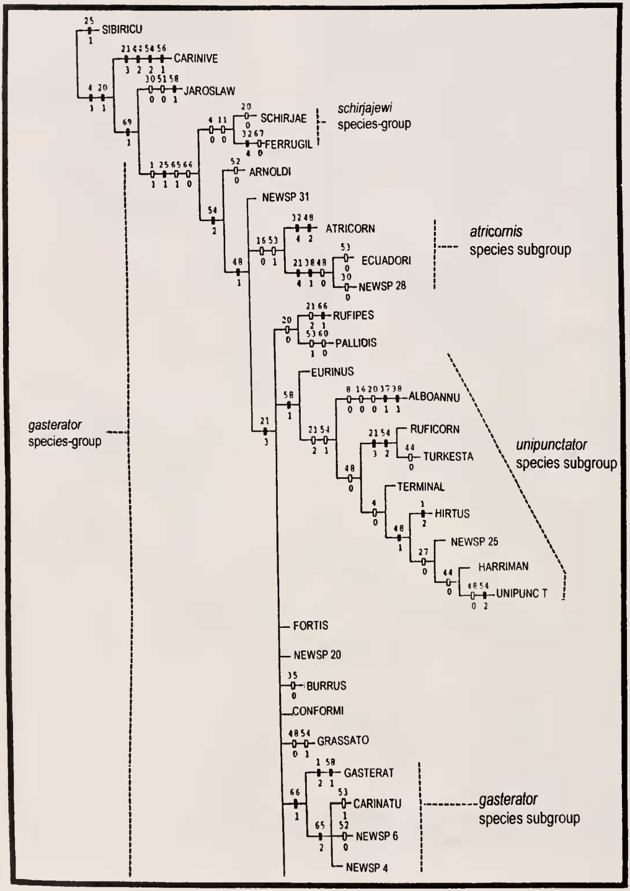

Fig. 7. The base of the apical species-group cluster of the derived section.

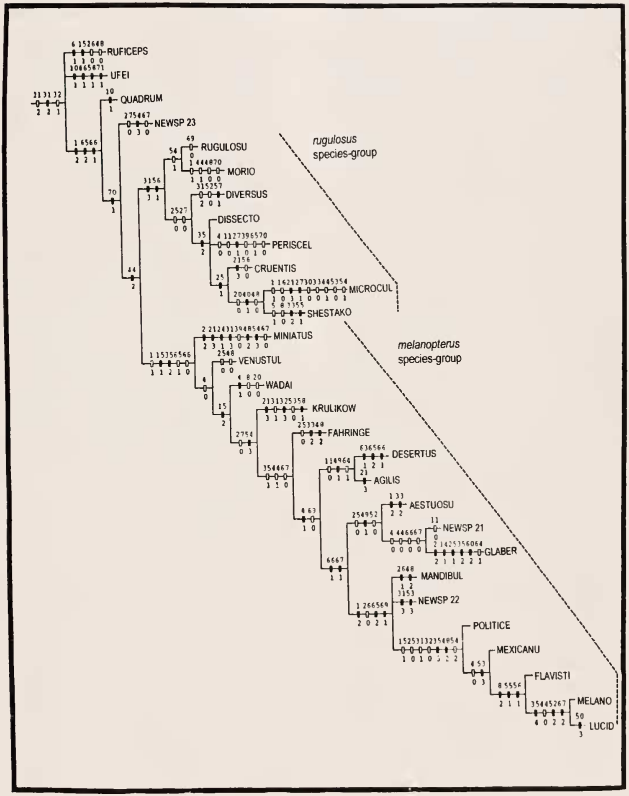

Fig. 8. The apex of the apical species-group cluster.

gasterator (Jurine), *A. rugulosus* (Nees von Esenbeck), *and A. melanopterus* (Erichson) species-subgroups.

The *A. gasterator* species-group is composed of *A. arnoldi* Tobias and new species 31 basally, and three species subgroups: the *A. atricornis* (Cresson), *A. gasterator* (Jurine), and *A. unipunctator* (Thunberg) species-subgroups. The group does not easily cluster based on any good synapomorphy. The retention of tarsal claw teeth basal only in the *A. gasterator* species-group distinguishes it from species-groups apicad to it. Although three species clusters exist within the *A. gasterator* species-group, they were considered subgroups, since they 1) clustered based on characters which reversed within the species-group or subgroup (*A. atricornis* species-subgroup); 2) were based on a color character, which are notoriously plastic across the genus (*A. unipunctator* species-subgroup), or 3) resulted in a paraphyletic group, such as the *A. unipunctator* species-subgroup, in which *A. eurinus* shares character states which define both the *A. unipunctator* and *A. gasterator* species-groups.

15. The ***ufei*** species-group (Fig. 8) is composed of one species, so far as known: A. *ufei* (Walley). The bicolored body is similar to the *A. unipunctator* species-subgroup, but the species differs in that the sides of the first metasomal tergite are parallel, and the female abdominal apex is compressed. Although this group is monospecific so far as known, it was given species-group status based on the unique metasomal features described above.
16. The ***rugulosus*** species-group (Fig. 8a) is monophyletic, and is defined by the uniquely shiny, coarsely and densely rugulopunctate vertex sculpturing and all black body. It consists of *A. cruentus* (Nees von Esenbeck), *A. dissector* (Nees von Esenbeck), *A. diversus* (Szepligeti), *A. microculatus* Watanabe, *A. morio* (Reinhard), *A. periscelis* (Reinhard), A. *rugulosus* (Nees von Esenbeck), and *A. shestakovi* (Shenefelt).
17. The ***melanopterus*** species-group (Fig. 8b) is monophyletic and is defined by the clypeo-antennal space/width of oral space ratio ≤ 0.69, scutal sculpturing excluding postero-medial dorsal surface smooth or finely punctate, and clypeus height/width less than 0.42. Members of the group are *A. aestuosus* (Reinhard), *A. agilis* (Telenga), *A. desertus* (Telenga), *A. fahringeri* (Telenga), *A. flavistigma* Shaw, *A. glaber* (Telenga), *A. krulikowskii* Kokoujev, *A. lucidus* (Szepligeti), *A. melanopterus* (Erichson), *A. mexicanus* Cresson, *A. mandibularis* (Cresson), *A. miniatus* (Herrich-Schaffer), *A. politiceps* (Gahan), *A. ruficeps* (Telenga), *A. venustulus* (Kokoujev), *A. wadai* (Watanabe), and new species 21, 22, and 23.

17a. The ***melanopterus*** species-subgroup (Shaw 1993, Fig 8b), a monophyletic subset of the above, consists of *A. flavistigma* Shaw, *A. lucidus* (Szepligeti), *A. mandibularis* (Cresson),. *A. melanopterus* (Erichson), *A. mexicanus* Cresson, *A. politiceps* (Gahan) and new species 23. The subgroup is defined by pectinate tarsal claws (Fig. 2c) and strongly protruding clypeal carina.

DISCUSSION OF HOST ASSOCIATION

The following data and that in Appendix I were drawn from Shenefelt (1975), Shaw (1983, 1994), and S. R. Shaw and P. M. Marsh (unpublished data). Of 208 *Aleiodes* species analyzed, host records were available for 40.4% of *Aleiodes* species. Host records were available for 65.4% of basal species, 27.3% of intermediate species, and 39.4% of derived species (Appendix I).

Basal species for which host associations were known either attacked host species from more than one family, or attacked hosts other than non-catocaline Noctuidae, Notodontidae, or Sphingidae. Exceptions were *A. gossypii*, *A. laphygmae*, *A. noc-*

turnus, and *A. nolophanae*. Two basal species in the *A. gastritor* species group (*A. pallescens* and *A. stigmator*) are gregarious.

Within intermediate species, the *A. coxalis* species-group showed a tendency to attack setose hosts within Arctiidae, Lasiocampidae, and Lymantriidae. *Aleiodes coxalis* species-group species comprise 50.0% of *Aleiodes* species known to attack arctiids and lymantriids. Of the 15 intermediate species with host records, 40% attack exclusively non-catocaline noctuids so far as known.

Within the derived section apicad of the *A. pulchripes* and *A. apicalis* species groups, only trifine Noctuidae are attacked so far as known. The *A. praetor* species-group attacks only sphingids. The *A. albitibia* species-group attacks only notodontids. Within the *A. pulchripes* species-group, geometrids, noctuids, and notodontids are attacked, so far as known.

Of the seven of 11 *A. apicalis* species-group species with known hosts, four attack plusiine noctuids (*A. brethesi, A. apicalis, A. molestus*, and *A. parasiticus*). One is associated with an unidentified noctuid mummy (*A. abdominalis*), and three attack non-noctuids.

Of all derived *Aleiodes* with host records, 69.7% attack trifine noctuids. Of the above except the *A. albitibia* and *A. praetor* species groups, 84.6% attack trifine noctuids.

Basal and intermediate species tend to have broad host ranges, and derived species tend to specialize on Noctuidae, Notodontidae, or Sphingidae. The only monophyletic groups which specialize on Notodontidae and Sphingidae lie at the base of the apical section. In the basal section, the *A. pallidator* species-group tends to specialize on Lymantriidae. The only *Aleiodes* species with host records for Catocalinae are in the *A. seriatus* species-group in the basal section. Among intermediate species, the *A. coxalis* species-group tends to specialize on setose hosts, especially arctiids and lymantriids.

According to the classification scheme of Nielsen and Common (1991), Noctuidae is the most derived lepidopteran family. The lepidopteran families Notodontidae, Lymantriidae, and Arctiidae are placed in superfamily Noctuoidea with Noctuidae. Notodontidae is the most basal noctuoid family (Nielsen and Common, 1991). Superfamily Sphingoidea, consisting of one family (Sphingidae), is immediately basal to Noctuoidea (Nielsen and Common, 1991).

Based on order of placement in a list of 19 subfamilies of Noctuidae, subfamily Catocalinae is placed within the four basal-most subfamilies (Nielsen and Common, 1991). Catocaline noctuids are utilized only by one *Aleiodes* species-group in the basal section, so far as known.

Family Arctiidae is placed just basad to the noctuid subfamilies referred to in the study (Nielsen and Common 1991). The only basal *Aleiodes* species known to attack arctiids are within the *A. seriatus* species-group.

Mitchell *et al.* have recently investigated the phylogeny of superfamily Noctuoidea by using characters derived from the nuclear gene EF-1α, which encodes elongation factor-1α protein (Mitchell *et al.* 1997). Based on their most parsimonious tree derived from all sites of EF-1α, the authors concluded that 1) Notodontidae comprises a monophyletic group at the base of Noctuoidea; 2) "quadrifine" Noctuidae comprise a paraphyletic group which consists of a monophyletic subgroup (Eutellinae, Nolinae, Sarrothripinae), and the basal-most subfamilies (Catocalinae, Herminiinae) of a more derived monophyletic group. Arctiidae and Lymantriidae are sister-groups at the apex of this latter monophyletic group; 3) the "trifine" noctuids, which comprise the remainder of Noctuidae, form a monophyletic group at the apex of the cladogram (Mitchell *et al.* 1997).

The findings of Mitchell *et al.* corroborate Nielsen and Common with respect to

Noctuoidea, except that Mitchell *et al.* find that Noctuidae is a paraphyletic group, with the quadrifine noctuids (including Catocalinae) more closely related to Arctiidae and Lymantriidae than to trifine noctuids (Mitchell *et al.* 1997). The latter finding is corroborated by Weller *et al.* (1994).

Since older koinobiont parasitoid species are thought to have broader host ranges while newer species are thought to have narrower ranges (Shaw 1994), and since this study provides evidence that basal and intermediate *Aleiodes* species have broader host ranges while derived species have narrower host ranges, the overall pattern of phylogenetic inferences made from morphological data in this study is corroborated by host association data in light of the above.

This study suggests that genus *Aleiodes* overall has co-evolved with its Lepidopteran hosts. Basal host families appear more likely to be attacked by basal *Aleiodes* species while the most derived host family, trifine Noctuidae, is more likely to be attacked by derived *Aleiodes* species. Non-derived groups with well defined synapomorphies such as the basal *A. seriatus* and *A. pallidator* species groups, and the intermediate *A. coxalis* species-group, appear to have co-evolved with noctuoid groups basal to trifine Noctuidae such as catocalines, lymantriids and arctiids. The exclusive associations of *Aleiodes* species within the derived section with specific host groups, such as that of the *A. praetor* species-group with sphingids, of the *A. albitibia* species-group with notodontids, and of *Aleiodes* species apicad of the *A. apicalis* and *A. pulchripes* species-groups with Noctuidae add weight to this co-evolutionary hypothesis.

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LITERATURE CITED

Achterberg, C. van. 1982. Notes on some type-species described by Fabricius of the subfamilies Braconinae, Rogadinae, Microgastrinae, and Agathidinae (Hymenoptera: Braconidae). *Entomologishche Berichten*, 42: 133–139.

Achterberg, C. van. 1985. Notes on Braconidae I–IV. *Zoologische Mededelingen* 59: 163–187.

Achterberg, C. van. 1991. Revision of the genera of the Afrotropical and W. Palearctic Rogadinae Foerster (Hymenoptera: Braconidae). *Zoologische Verhandelingen* 273: 3–102.

Achterberg, C. van. 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandelingen* 283: 3–189.

Achterberg, C. van. 1993 Generic revision of the subfamily Betylobraconinae (Hymenoptera: Braconidae) and other groups with modified fore tarsus. *Zoologische Verhandelingen* 298: 3–242.

Achterberg, C. van and A. M. Penteado-Dias. 1995. Six new species of the *Aleiodes dispar* group (Hymenoptera: Braconidae: Rogadinae). *Zoologische Mededelingen Leiden* 69: 1–18.

Farris, J. S. 1970. Methods for computing Wagner trees. *Systematic Zoology* 19: 83–92.

Farris, J. S. 1988. *Hennig86 reference, version 1.5.* Port Jefferson, New York.

Harris, R. A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–33.

Hennig, W. 1966. *Phylogenetic Systematics.* John Wiley and Sons. New York.

Hennig, W. 1981. *Insect Phylogeny.* John Wiley and Sons. New York.

Huber, J. and M. Sharkey. 1993. Chapter 3. Structure. *In*: Hymenoptera of the World: An Identification Guide to Families (ed. by H. Goulet and J. T. Huber). Agriculture Canada Publication 1894/E. Ottawa.

Lipscomb, D. L. 1992. Parsimony, Homology and the Analysis of Multistate Characters. *Cladistics* 8: 45–65.

Marsh, P. 1979. The braconid (Hymenoptera) parasites of the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). *Annals of the Entomological Society of America* 72: 794–810.

Marsh, P. M. and S. R. Shaw 1998. Revision of North American *Aleiodes* Wesmael (Part 3): the *seriatus* species-group in the New World (Hymenoptera: Braconidae, Rogadinae). *Proceedings of the Entomological Society of Washington* 100: 395–408.

Mickevich, M. F. 1982. Transformation series analysis. *Systematic Zoology* 31: 461–478

Mickevich, M. F. and D. Lipscomb. 1991. Parsimony and the choice between different transformations for the same character set. *Cladistics* 7: 111–139.

Mickevich, M. F. and S. J. Weller. 1990. Evolutionary character analysis: tracing character change on a cladogram. *Cladistics* 6: 137–170.

Mitchell, A., S. Cho, J. C. Regier, C. Mitter, R. W. Poole, and M. Matthews. 1997. Phylogenetic utility of elongation factor-1α in Noctuoidea (Insecta: Lepidoptera): The limits of synonymnous substitution. *Molecular Biology and Evolution* 14(4); 381–390.

Mitter, C. and E. Silverfine. 1988. On the systematic position of *Catocala* Schrank (Lepidoptera: Noctuidae). *Systematic Entomology* 13: 67–84.

Nielsen, E. S. and I. F. B. Common. 1991. Chapter 41. Lepidoptera. In: *The Insects of Australia*. Cornell University Press, Ithaca, New York.

Nixon, K. C. 1991. *CLADOS Version 1.0*. Cornell University, Ithaca, New York.

Shaw, M. 1983. On(e) the evolution of endoparasitism: the biology of some genera of Rogadinae (Braconidae). *Contributions of the American Entomological Institute* 20: 307–328.

Shaw, M. 1994. Chapter 7. Parasitoid host ranges. *in Parasitoid Community Ecology*. (ed. by B.A. Hawkins and W. Sheehan). Oxford University Press, Oxford, Great Britain.

Shaw, M. and T. Huddleston. 1991. Classification and biology of braconid wasps. *Handbooks for the Identification of British Insects Vol. 7, Part II* 7: 1–126.

Shaw, S. R. 1993. Systematic status of *Eucystomastax* Brues and characterization of the Neotropical species. *Journal of Hymenoptera Research* 2: 1–11.

Shaw, S. R. 1995. Chapter 12.2. Braconidae. In: *The Hymenoptera of Costa Rica* (ed. by P. Hanson and I. D. Gauld). Oxford University Press, Oxford, Great Britain.

Shaw, S. R., P. M. Marsh, and J. C. Fortier. 1997. Revision of North American *Aleiodes* Wesmael (Part 1): the *flavidus* Cresson species-group in the New World (Hymenoptera: Braconidae, Rogadinae). *Journal of Hymenoptera Research* 6: 10–35.

Shaw, S. R., P. M. Marsh, and J. C. Fortier. 1998a. Revision of North American *Aleiodes* Wesmael (Part 2): the *apicalis* (Brulle) species-group in the New World (Hymenoptera: Braconidae, Rogadinae). *Journal of Hymenoptera Research* 7: 62–73.

Shaw, S. R. and P. M. Marsh. 1998b. Revision of North American *Aleiodes* Wesmael (Part 4): the *praetor* and *albitibia* groups in the New World (Hymenoptera:Braconidae, Rogadinae). *Proceedings of the Entomological Society of Washington* 100: 553–565.

Shenefelt, R. D. 1969. Notes on some rogadine genera (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 71: 428–444.

Shenefelt, R. D. 1975. Braconidae 8. Exothecinae, Rogadinae. *Hymenopterorum Catalogus* (nova editio) 12: 1163–1262.

Schuh, R. T. 1991. Phylogenetic, host and biogeographic analyses of the Pilophorini (Heteroptera: Miridae: Phylinae). *Cladistics* 7: 157–189.

Weller, S. J., D. P. Pashley, J. A. Martin, and J. L. Constable. 1994. Phylogeny of noctuoid moths and the utility of combining independent nuclear and mitochondrial genes *Systematic Biology* 43: 194–211.

Whitfield, J. B. 1992. The polyphyletic origin of endoparasitism in the cyclostome lineages of Braconidae (Hymenoptera). *Systematic Entomology* 17: 273–286.

Wiley, E. O. 1981. *Phylogenetics; the Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, Inc. New York.

Appendix I. List of *Aleiodes* species examined.

Aleiodes species	Host family(ies)
abdominalis Cresson 1869	Noctuidae
aciculatus Cresson 1869	Noctuidae
aestuosus (Reinhard) 1863	Noctuidae (Noctuinae, Ophiderinae)
agilis (Telenga) 1941	unknown
albitibia (Herrich-Schaffer) 1838	Notodontidae
alboannulatus Belokobylskyj	unknown
alutaceus Granger 1949	unknown
aligharensi (Quadri) 1933	Gelechiidae, Noctuidae, Notodontidae
alternator (Nees von Esenbeck) 1934	Arctiidae, Lasiocampidae, Lymantriidae
angustatus (Papp) 1969	unknown
annulatus Granger 1949	unknown
antennatus Belokobylskyj 1996	unknown
apicalis (Brulle) 1832	Arctiidae, Geometridae, Lasiocampidae, Noctuidae (Hadeninae, Plusiinae)
arcticus Thomson 1891	unknown
arizoniensis Marsh and Shaw 1997	unknown
armatus Wesmael 1838	Geometridae, Noctuidae
arnoldii Tobias 1976	unknown
atriceps Cresson 1869	unknown
atricornis (Cresson) 1872	Noctuidae (Hadeninae)
autographae (Viereck) 1910	Noctuidae
bakeri (Brues) 1912	unknown
bicolor (Spinola) 1808	Geometridae, Lycaenidae, Lymantriidae, Noctuidae, Nymphalidae, Pterophoridae, Zygaenidae
borealis Thomson 1891	unknown
brethesi (Shenefelt) 1909	Noctuidae (Plusiinae)
brevipendulatus Achterberg and Penteado-Dias, 1995	unknown
breviradialis Granger 1949	unknown
buoculus Marsh 1989	unknown
burrus Cresson 1869	Noctuidae (Acronictinae, Noctuinae)
cameronii (Dalla Torre) 1898	Notodontidae
cantherius (Lyle) 1919	Geometridae
carinatus (Ashmead) 1888	unknown
cariniventris (Enderlein) 1912	unknown
caucasicus Tobias 1976	unknown
cazieri Marsh and Shaw 1997	unknown
chloroticus Shestakov 1940	unknown
circumscriptus (Nees von Esenbeck) 1834	Bombycidae, Geometridae, Lymantriidae, Noctuidae, Notodontidae, Psychidae, Pyralidae, Tortricidae
compressor (Herrich-Schaffer) 1838	Gelechiidae, Geometridae, Limacodidae, Noctuidae, Notodontidae
conformis (Muesebeck) 1960	unknown
convexus Achterberg 1991	unknown
coxalis (Spinola) 1808	Hesperiidae, Satyridae
coxator Telenga 1941	unknown
crassipes Thomson 1891	unknown
cruentis (Nees von Esenbeck) 1834	Noctuidae (Hadeninae), Lymantriidae
curtispina Granger 1949	unknown
dendrolimi (Matsumura) 1925	Lasiocampidae
desertus (Telenga) 1941	unknown
dispar (Curtis) 1834	Noctuidae, Nymphalidae
dissector (Nees von Esenbeck) 1834	Noctuidae (Acronictinae, Hadeninae)
diversicornis Granger 1949	unknown
diversus (Szepligeti) 1903	Noctuidae (Acronictinae, Hadeninae)

Appendix 1. Continued.

Aleiodes species	Host family(ies)
earinos Marsh and Shaw 1997	unknown
ecuadoriensis (Brues) 1926	unknown
eurinus (Telenga) 1941	unknown
excavatus (Telenga) 1941	unknown
fahringeri (Telenga) 1941	unknown
femoratus Cresson 1869	unknown
ferrugileti (Shenefelt) 1975	unknown
flavidus (Cresson) 1865	unknown
flavistigma Shaw 1993	Unknown
flavitarsus Marsh & Shaw 1998	Noctuidae
fortipes (Reinhard) 1863	unknown
fortis (Muesebeck) 1960	unknown
fuscipennis (Szepligeti) 1904	unknown
gasterator (Jurine) 1807	Noctuidae (Plusiinae)
gastritor (Thunberg) 1822	Choreutidae, Drepanidae, Geometridae, Incurvariidae, Notodontidae
geometrae (Ashmead) 1888	Geometridae
glaber (Telenga) 1941	unknown
gossypii (Muesebeck) 1960	Noctuidae
grandis Giraud 1857	Noctuidae (Acronictinae)
granulatus (De Gant) 1930	Noctuidae
graphicus Cresson 1872	Sphingidae
grassator (Thunberg) 1822	unknown
gressitti (Muesebeck) 1964	unknown
harrimani (Ashmead) 1902	unknown
hellenicus Papp 1985	unknown
hirtus (Thomson) 1891	unknown
incertoides Telenga 1941	unknown
incertus Kokoujev 1898	unknown
indiscretus (Reardon)	Lymantriidae
jakolewi Kokoujev 1898	unknown
krulikowskii Kokoujev 1898	unknown
kuslitzkyi Tobias 1976	unknown
laphygmae (Viereck) 1912	Noctuidae
longicornis Granger 1949	unknown
longipendulatus Achterberg and Penteado-Dias 1995	unknown
lucidus (Szepligeti) 1906	unknown
lymantriae (Watanabe) 1937	Lymantriidae
malacosomatos (Mason) 1979	Lasiocampidae
mandibularis (Cresson) 1872	unknown
medianus (Thomson) 1896	unknown
melanopterus (Erichson) 1848	unknown
mexicanus Cresson 1869	unknown
microculatus (Watanabe) 1937	unknown
miniatus (Herrich-Schaffer) 1838	unknown
modestus (Reinhard) 1863	Geometridae, Lasiocampidae
moldavicus Tobias 1986	unknown
molestus (Cresson) 1872	Noctuidae (Plusiinae, Noctuinae)
morio (Reinhard) 1863	Noctuidae
narangae (Rohwer) 1934	unknown
negativus Tobias 1960	Noctuidae
neotropicalis (Shenefelt) 1975	unknown
nigribasis (Enderlein) 1918	unknown
nigricornis Wesmael 1838	Noctuidae, Pyralidae, Geometridae

Appendix 1. Continued.

Aleiodes species	Host family(ies)
nigristemmaticum (Enderlein) 1918	Noctuidae (Catocalinae)
nocturnus Tobias 1960	Noctuidae
nolophanae (Ashmead) 1888	Noctuidae
notozophus Marsh and Shaw 1997	unknown
nunbergi Noskiewicz 1956	Geometridae
pallescens Hellen 1927	Noctuidae, Notodontidae (gregarious)
pallidator (Thunberg) 1822	Gelechiidae, Geometridae, Lymantriidae, Noctuidae, Psychidae, Tortricidae
pallidistigmus (Telenga) 1941	unknown
palmatus (Walley) 1941	Noctuidae
parasiticus Norton 1869	Noctuidae
pedalis Cresson 1869	unknown
pellucens (Telenga) 1941	unknown
percurrens (Lyle) 1921	Noctuidae (Catocalinae, Acronictinae)
perinetensis (Shenefelt) 1975	unknown
periscelis (Reinhard) 1863	unknown
perplexus (Gahan) 1917	Geometridae, Noctuidae
pictus (Herrich-Schaffer) 1838	unknown
platypterygis (Ashmead) 1888	Drepanidae
plurilineatus (Cameron) 1911	unknown
politiceps (Gahan) 1917	Noctuidae (Hadeninae, Noctuinae)
praetor (Reinhard) 1863	Sphingidae
procerus Wesmael 1838	unknown
pulchripes Wesmael 1838	Lasiocampidae, Lymantriidae, Noctuidae (Acronictinae), Notodontidae
punctipes Thomson 1891	unknown
quadrum Tobias 1976	unknown
quebecensis (Provancher) 1880	Noctuidae (Acronictinae)
rileyi Cresson 1869	Lymantriidae, Noctuidae (Acronictinae, Hadeninae), Pyralidae
rogezensis Granger 1949	unknown
rossi Marsh and Shaw 1997	unknown
rossicus Kokoujev 1898	Drepanidae, Geometridae, Lasiocampidae, Lymantriidae, Noctuidae, Pyralidae
ruficeps (Telenga) 1941	unknown
rutficornis (Herrich-Schaffer) 1838	Lasiocampidae, Lymantriidae, Noctuidae (Hadeninae, Noctuinae, Plusiinae)
rufipes (Thomson) 1891	unknown
rugosicostalis Achterberg and Penteado-Dias, 1995	unknown
rugulosus (Nees von Esenbeck) 1811	Noctuidae (Acronictinae)
sanctihyacinthi (Provancher) 1880	Arctiidae
sanctivincentensis (Shenefelt), 1975	unknown
satanas Telenga 1941	unknown
schirjajewi (Kokoujev) 1899	unknown
scriptus (Enderlein) 1918	unknown
scrutator (Say) 1836	Choreutidae, Incurvariidae, Notodontidae
seriatus (Herrich-Schaffer) 1838	Arctiidae, Lyonitiidae, Noctuidae
shestakovi (Shenefelt) 1975	unknown
sibiricus (Kokoujev) 1903	unknown
signatus (Nees von Esenbeck) 1911	unknown
similis (Curtis) 1834	unknown
simillimus (Ashmead) 1889	Geometridae
stigmator (Say) 1824	Geometridae, Lasiocampidae, Lymantriidae, Noctuidae (gregarious)

Appendix I. Continued.

Aleiodes species	Host family(ies)
sudatorius Papp 1985	unknown
tatianae (Telenga) 1941	unknown
testaceus (Telenga) 1941	unknown
terminalis (Cresson) 1869	Noctuidae (Acronictinae, Hadeninae, Noctuinae)
Tetrasphaeropyx Ashmead 1888 spp.	Geometridae
texanus (Cresson) 1869	Sphingidae
transversestriatus Granger 1949	unknown
tristis Wesmael 1838	unknown
turkestanicus (Telenga) 1941	unknown
ufei (Walley) 1941	Noctuidae (Noctuinae)
ungularis Thomson 1891	unknown
unicolor Wesmael 1838	unknown
unipunctator (Thunberg) 1822	Noctuidae (Acronictinae, Hadeninae)
vaughani (Muesebeck) 1960	Noctuidae (Acronictinae)
venustulus (Kokoujev) 1905	unknown
wadai (Watanabe) 1937	unknown
xanthus (Marshall) 1892	unknown
new species 1	unknown
new species 2	Lymantriidae
new species 3	Noctuidae
new species 4	unknown
new species 5	unknown
new species 6	unknown
new species 7	unknown
new species 8	Sphingidae
new species 9	unknown
new species 10	Lycaenidae
new species 11	unknown
new species 12	unknown
new species 13	unknown
new species 14	Notodontidae
new species 15	unknown
new species 16	unknown
new species 27	unknown
new species 18	unknown
new species 19	unknown
new species 20	unknown
new species 21	unknown
new species 22	unknown
new species 23	unknown
new species 24	unknown
new species 25	Noctuidae (Cuculliinae)
new species 26	Arctiidae
new species 27	unknown
new species 28	Noctuidae (Hypeninae)
new species 29	Sphingidae
new species 30	unknown
new species 31	unknown
new species 32	Lycaenidae
new species 33	unknown
new species 34	unknown
new species 35	unknown
new species 36	unknown
new species 37	Lymantriidae
new species 38	Geometridae